The conservation and management of biodiversity are crucial for achieving poverty reduction and sustainable development. India is a biodiversity-rich nation that supports 18% of the world's population on only 2.4% of the world's total land area. Remarkably, it holds parts of four global biodiversity hotspots that have high concentrations of endemic taxa and some of the biggest remaining wild populations of large, wide-ranging mammals. India faces unique and difficult challenges in balancing the conservation of its great biological wealth with the enhancement of human development and well-being. Climate change adds an overarching dimension to this challenge. Climate change is widely expected to have multiple adverse impacts on biodiversity, with negative consequences for human well-being. However, biodiversity, through the ecosystem services it supports, is essential to both climate change mitigation and adaptation. Preserving biological diversity at every level, from genes to biomes, is the most effective way of facilitating the rapid changes necessary for human societies to adapt to future climate change. Owing to its tremendous diversity of human and biological systems, India is well-positioned to meet this challenge.

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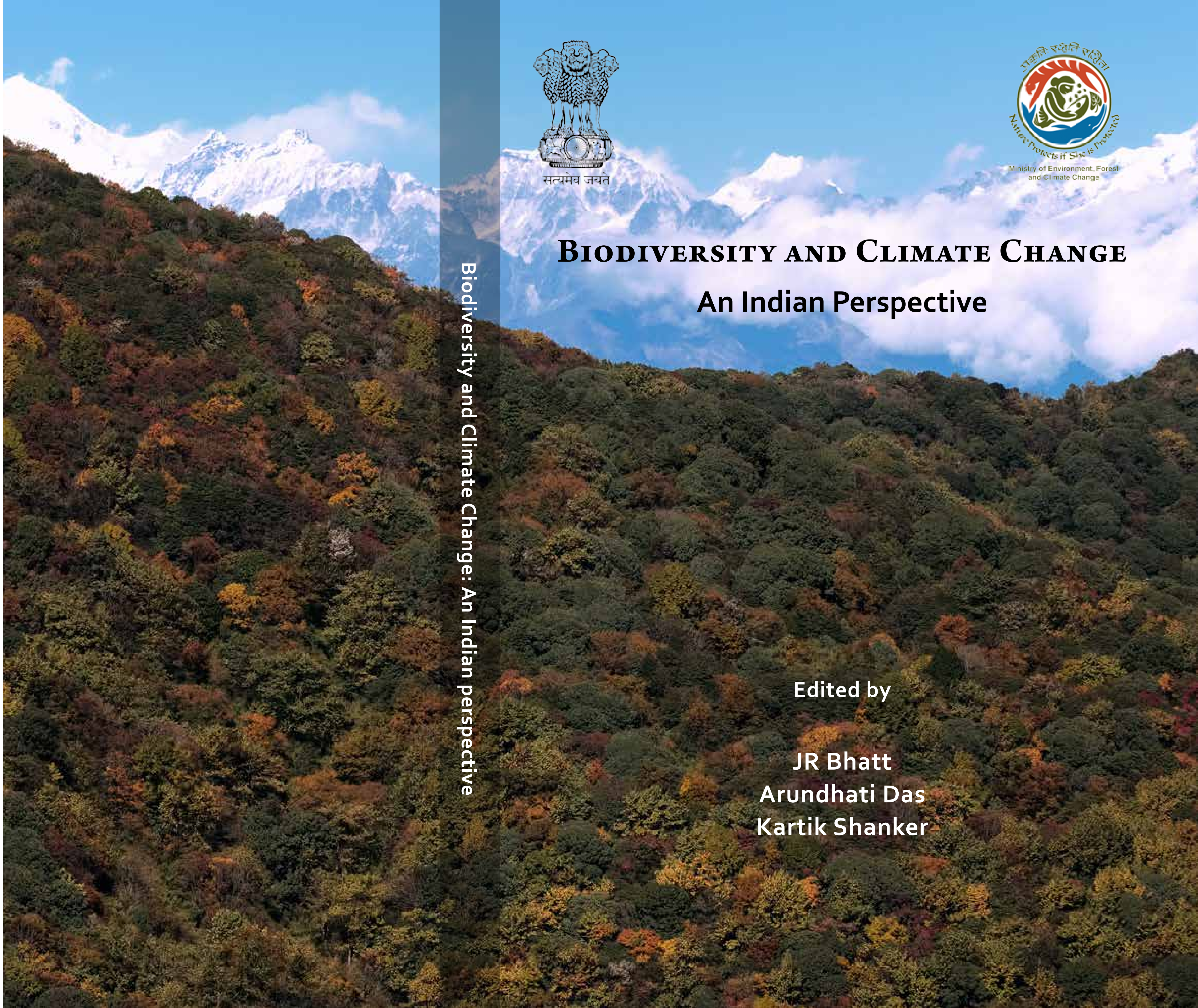

Biodiversity and Climate Change: An Indian perspective

सत्यमेव जयते

Ministry of Environment, Forest
and Climate Change

BIODIVERSITY AND CLIMATE CHANGE

An Indian Perspective

Edited by

JR Bhatt
Arundhati Das
Kartik Shanker

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भारत सरकार
पर्यावरण, वन एवं जलवायु परिवर्तन मंत्री
GOVERNMENT OF INDIA
MINISTER OF ENVIRONMENT, FOREST & CLIMATE CHANGE

MESSAGE

It gives me immense pleasure to share the Indian perspective on biodiversity and climate change with the global community on the occasion of the 24th meeting of the Conference of Parties (COP) to the United Nations Framework Convention on Climate Change (UNFCCC) at Katowice, Poland in December 2018.

India is a recognized megadiverse country rich in biodiversity and associated traditional knowledge. With only 2.4% of the world's land area, India harbours 7-8% of the recorded species diversity, while supporting nearly 18% of the human population and a similar percentage of cattle population. There is a need to meet the extant developmental challenges as well as manage the biotic pressure. Climate change further exacerbates and adds to our challenges and the pressure. Climate change has impacted the distribution, growth and timing of seasonal activities of many plant species while posing threats to salt marshes, mangroves, seagrass beds, and coral reefs . Degradation of biodiversity impacts ecosystem services which directly and adversely affect local livelihoods and in turn national economy and security.

With this backdrop, India accords high priority to conservation of biodiversity for long-term ecological, environmental, economic, food and nutritional security. India has a robust National Biodiversity Strategy and we have actually surpassed achieving the global Aichi target of 17% of terrestrial area-based conservation. In the area of green cover, it is a matter of satisfaction that despite multiple challenges, in 2017 the overall tree and forest cover stands at 24.39% of the total geographical area and about 12% of country's greenhouse gas (GHG) emissions are offset by the forestry sector. India has not only been able to sustain but also increase its mangrove cover when these ecosystems are disappearing at an alarming rate across the world. India has also done well in the field of wildlife conservation. The population of tiger, elephant, rhino and other wildlife is on the rise. All these initiatives go on to show that development can be environment-friendly and need not come at the cost of our green assets.

Climate change is a global problem. India's both per capita and cumulative GHG emissions are low. However, our population is at the receiving end by climate change impacts. The poor are the worst affected. India as a responsible global partner is doing its bit but global problems like climate change call for global action.

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MINISTER OF ENVIRONMENT, FOREST & CLIMATE CHANGE

The global climate action should be as per the principle of Common but Differentiated Responsibilities and Respective Capabilities, Equity and Climate Justice. I understand from the available scientific studies that still there is a chance to protect biodiversity on earth if concerted time-bound actions are undertaken by the global community.

Biodiversity is Life, and its conservation and sustainable management are essential to achieving the Aichi Biodiversity Targets and Sustainable Development Goals. India is committed to Sustainable Development Goals. India is a firm believer in multilateralism and looks forward to the appropriate implementation of various facets of the Paris Agreement in letter, spirit and concerted global action. Indian Government under the able and visionary leadership of Hon'ble Prime Minister Shri Narendra Modi is committed to engage and support outcome-oriented discussions and actions under the Paris Agreement. The deliberations at the 14th meeting of COP to Convention on Biological Diversity give hope for responding to the impacts of climate change on biodiversity. This hope could be strengthened further at Katowice if the developed countries agree to act and save biodiversity on earth by providing new and additional financial and technical support to developing countries to cope up and adapt to climate change.

I congratulate all those involved in this assignment, in particular, the contributing authors. This book is both engaging, informative and is purposed to kindle the interest among all stakeholders fathoming biodiversity and climate change inter-linkages in India.

Harsh

Date: 28.11.2018

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MINISTRY OF ENVIRONMENT, FOREST AND CLIMATE CHANGE

FOREWORD

Sustainable management of biological resources is fundamental for ensuring the country's overall food, nutritional and strategic security. India's management of its natural wealth is crucial to protecting global biodiversity and meeting Sustainable Development Goals. This book titled "Biodiversity and Climate Change – An Indian Perspective" showcases India's work on the impact of climate change on biodiversity and associated ecosystem services.

For a developing country like India with limited resources and demanding developmental imperatives, climate change is an additional burden. There is certainty regarding the fact that we now face a warmer future with the threat of extreme weather events. This is particularly true, given the impacts of factors such as habitat loss and spread of invasive species that are already affecting these systems. The effects of climate change on our ecosystems though less understood have already started affecting the local production systems and population. The book documents the impacts of climate change on ecosystem services especially pollination, bird migration, marine & coastal, forest, human-wildlife conflict, urban ecology among others. These impacts of climate change are both visible and significant.

The cost of conserving natural resources is huge and requires sustained efforts. The Government of India's growth strategy is based on the principle of development without destruction and '*sab ka sath sab ka vikas*'. India's National Biodiversity Action Plan takes into account the impact of climate change on its biological diversity. Several sector-specific schemes and programs are increasingly accounting for climate variability. However, the on-ground implementation of these measures requires enhanced and sustained financial support.

India is committed to mitigating climate change by expanding forest and tree cover, through reforestation and afforestation, to sequester an additional 2.5-3 billion tonnes of carbon by 2030 as per our Nationally Determined Contributions. Because of the threat of climate change, humanity is today beset with the problem of the very existence of the human species and the myriad life forms on earth. The problem of climate change is global and can't be solved by an individual or a nation. Only a global consensus with all of mankind's intellect, ingenuity, skills, imagination and dedication roused and fused into a massive emergency operation to preserve earth's beauty, and bounty in terms of climate and biodiversity can take humans out of the present predicament.

The contribution of eminent subject experts from India has enriched this volume and is appreciated. I compliment the contributing authors and appreciate the efforts put in by Dr. Arun Kumar Mehta, Additional Secretary and Dr. J. R. Bhatt, Scientist G, Ministry of Environment, Forest and Climate Change in bringing out this valuable publication.

[C.K. Mishra]

Dated: **29th November, 2018**
Place: **New Delhi**

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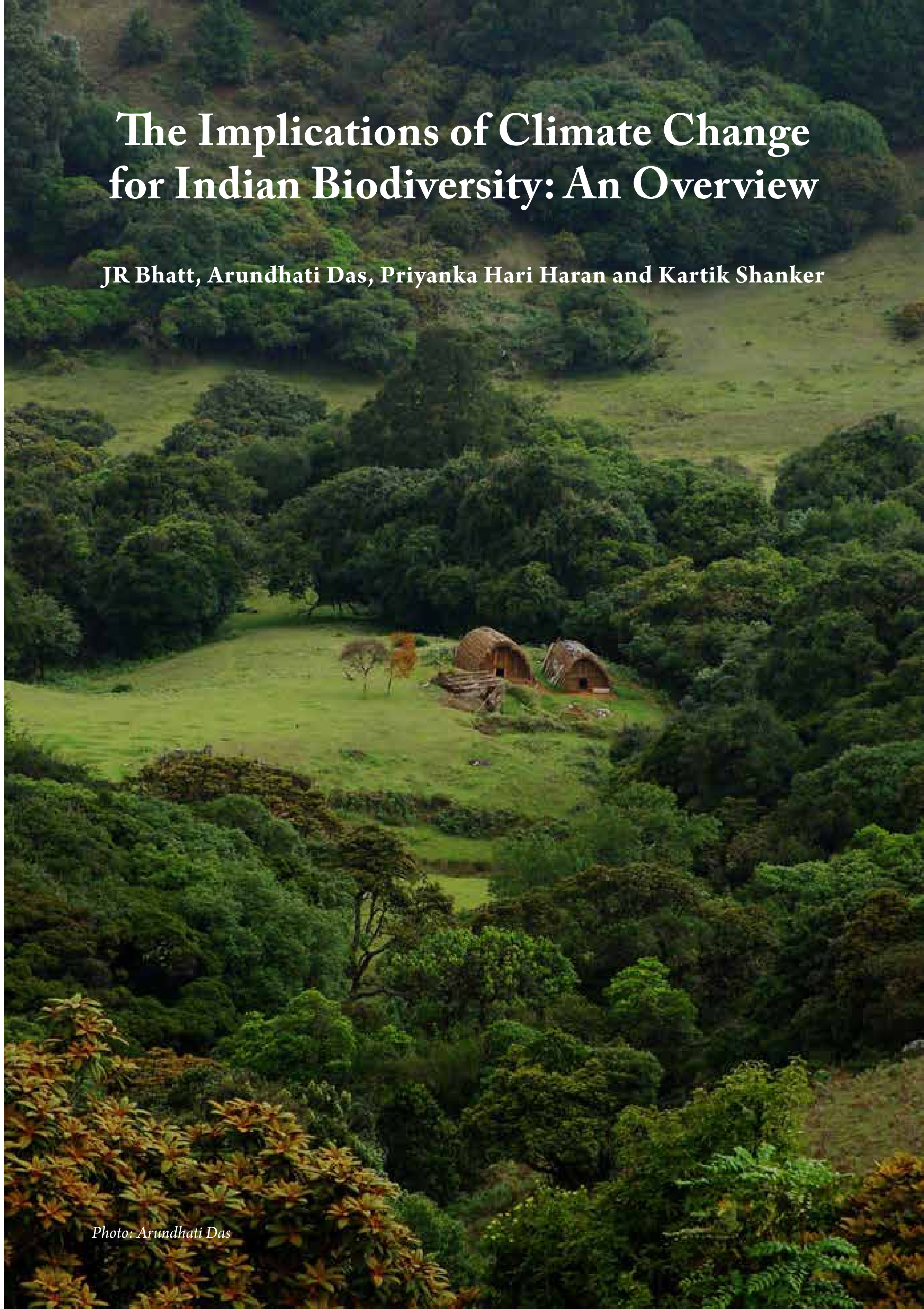

The Implications of Climate Change for Indian Biodiversity: An Overview

JR Bhatt, Arundhati Das, Priyanka Hari Haran and Kartik Shanker

Photo: Arundhati Das

INTRODUCTION

The conservation and management of biodiversity are crucial for achieving poverty reduction and sustainable development (Millennium Ecosystem Assessment 2005). India is a biodiversity-rich nation that supports 18% of the world's population on only 2.4% of the world's total land area. Remarkably, it holds parts of four global biodiversity hotspots that have high concentrations of endemic taxa (Myers 2003) and some of the biggest remaining wild populations of large, wide-ranging mammals (Sukumar 1989; Ranganathan et al. 2008). The country faces unique and difficult challenges in balancing the conservation of its great biological wealth with the enhancement of human development and well-being. Climate change adds an overarching dimension to this challenge. Climate change is widely expected to have multiple adverse impacts on biodiversity, and human well-being. Biodiversity, through the ecosystem services it supports, is essential to both climate change mitigation and adaptation. Preserving biological diversity at every level, from genes to biomes, is the most effective way of facilitating the rapid changes necessary for human societies to adapt to future climate change. Owing to its tremendous diversity of human and biological systems, India is well-positioned to meet this challenge.

PURPOSE OF THE REPORT

The objective of this report is to review the current state of knowledge on the impact of climate change on Indian biodiversity. It is one of a series of such reports that deal with the effects of climate change on various environmental and natural resources that are important for human well-being. Apart from biodiversity, these include freshwater, forestry, agriculture, marine and coastal resources, mountains and glaciers, urban areas and human health.

In this chapter, we provide an overview of how biodiversity underpins the linkage between all these sectors and human well-being, and how climate change could affect these links. We then introduce the report on climate change and biodiversity. We synthesise the conclusions from each chapter, regarding how climate change could potentially affect different levels of organization of natural ecosystems from individual organisms to species, communities and entire biomes. Finally, we identify critical knowledge gaps and present recommendations for conserving biodiversity in the face of climate change.

THE POTENTIAL IMPLICATIONS OF CLIMATE CHANGE IMPACTS ON BIODIVERSITY

Biodiversity is not only crucial to ecosystem functioning, but also plays a role in protection from natural disasters. Extreme weather events such as storms and flooding are projected to become more pervasive threats due to climate change, as is sea level rise. Adger et al. (2005) emphasize the importance of building resilience to natural disasters, particularly in coastal regions. The diversity of responses in various species that perform the same ecosystem function is a critical factor in maintaining ecosystem resilience to changes in the environment, particularly when ecosystems are reorganising (Elmqvist et al. 2003). Munang et al. (2013) list natural hazard mitigation as an important regulating service that ecosystems offer, especially now, when weather patterns are becoming increasingly unpredictable due to climate change. If ecosystems are managed in a way that conserves biodiversity, the effects of flooding, landslides, wildfires, droughts and storm surges can be mitigated more effectively.

For example, mangrove forests which serve as breeding sites and nursing grounds for crustaceans, fish and reptiles and provide livelihoods to local communities, have been found to lessen tsunami impacts (Danielsen et al. 2005; Kathiresan and Rajendran 2005). However, marine and coastal habitats, and mangroves in particular, are at risk of being lost due to rising sea levels (Jagtap and Nagle 2007). Coral reefs, like mangroves, are habitat-forming species for thousands of other species in oceans (Hoegh-Guldberg and Bruno 2010). Increased sea surface temperatures can have adverse effects on corals, and can cause them to bleach and die (Cinner et al. 2012). Further, resilience and recovery after cyclones and bleaching events are hampered in corals affected by reduced herbivory and excessive nutrients (Hughes et al. 2003). In fact, corals might move away from low latitudes in the future, and their place could be taken by algae and sponges, which would result in a loss of productivity in fisheries in tropical regions (Bell et al. 2013). Ecosystem services and functions are positively correlated to marine species diversity (Worm et al. 2006). Growth, survival and reproduction of fish stocks may be affected due to climate change, thereby reducing the productivity of marine ecosystems (Brander 2007).

Freshwater resources are also expected to be affected by climate change. Studies have shown that soil and water nutrients are more effectively mobilized in ecosystems that support more species, compared to those that support fewer species (Tilman et al. 1996; Bracken and Stachowicz 2006). Climate change threatens water resources via changes in flow regimes and increased air temperature (Heino et al. 2009; Whitehead et al. 2009). Finding a balance between the multiple ways rivers can be used (e.g., to maintain ecological functions and generate electricity) is tricky (Renöfält et al. 2010), and the changing climate only makes the need for such balance more urgent (Palmer et al. 2008).

Photo: Arundhati Das

Similar challenges are prevalent in forest management. Biodiversity in forests is closely (positively) related to ecosystem productivity, stability and resilience (Thompson et al. 2009), and tropical forests are among the most biologically diverse and productive ecosystems on earth. They provide important ecosystem services at regional and global scales (Malhi et al. 2008), including the production of oxygen and climate regulation, besides acting as major carbon sinks. Carbon sequestration could be dramatically lowered if such forests are lost at large scales (Cramer et al. 2004). Climate change is likely to lead to loss of biodiversity (Rull and Vegas-Vilarrúbia 2006), which in turn would lead to an accelerated rate of decrease in productivity (Liang et al. 2016), thus affecting the flow of goods and services from forests.

In urban areas, vegetation can help reduce the heat island effect (Chang et al. 2007). Urban warming leads to increased consumption of energy for cooling – an indirect feedback to climate change (Grimm et al. 2008). Gardens in cities host many reptiles, mammals, birds, insects and other invertebrates (Jaganmohan et al. 2012), and such natural areas are important for quality of life, for their environmental, psychological and social services (Chiesura 2004). Cities are already seeing increases in CO_2, ozone, temperature and other factors that will increase in non-urban areas in the coming decades (Carreiro and Tripler 2005). Moreover, urban greenery can sequester significant amounts of carbon (Pickett et al. 2008) and, if well planned, even small areas of vegetation can offer key ecosystem services (Dearborn and Kark 2010).


Photo: ATREE

Access to greenery has been linked to longevity (Takano et al. 2002) and self-reported health (de Vries et al. 2003). The ecosystem services provided by such green spaces provide healthy environments for people, and could provide socio-economic benefits to communities (Tzoulas et al. 2007). Through its impacts on biodiversity, climate change could impair ecosystem services and goods that contribute to human health. Short-term variations in temperature and precipitation could impact diarrhoea occurrence, malaria and dengue, via changes in the distribution of vectors (Haines et al. 2006). Climate change effects on human health are anticipated to be mostly negative. For example, extreme events like floods, droughts and heat waves could have direct and instantaneous effects on human mortality, in addition to long-term effects. In addition, biodiversity loss increases spread of pathogens and disease prevalence (Keesing et al. 2010), and soil biodiversity plays a role in disease control, while also helping to ensure food, air and water quality and supply (Wall and Six 2015).

In addition to changing the disease pressure from various food-borne diseases, food safety conditions could be altered with changing climate (Schmidhuber and Tubiello 2007). In particular, the impacts of changes in precipitation and temperature pose significant threats to food security (Schmidhuber and Tubiello 2007). While there will be some positive effects due to higher CO_2 and temperature, they must be weighed against negative effects such as expanded pest ranges and compromised food security (Schmidhuber and Tubiello 2007). Increased frequency of extreme events could also adversely affect crop yield (Schmidhuber and Tubiello 2007; Sunderland 2011). Biodiversity provides a safety-net in times of reduced agricultural production (Karjalainen et al. 2010) and during vulnerable periods resulting from climatic factors (Cotter and Tirado 2008). In general, components of biodiversity are responsible for the maintenance of ecological processes that are vital for agriculture – soil fertility, nutrient cycling, disease and pest control, and pollination and seed dispersal (Thrupp 2000).


Photo: Samson, ATREE

FROM INDIVIDUALS TO COMMUNITIES: IMPACTS AND VULNERABILITY

Average global temperature has increased by 0.85°C since the mid-19th century, with the vast majority (>90%) of additional heat being stored in the oceans (IPCC 2014). Global hydrological cycles have changed, with an increase in average precipitation over mid-latitudes in the Northern Hemisphere and shifts in ocean salinity further toward extremes, since the 1950s (IPCC 2014). Glaciers are shrinking, and the Greenland and Antarctic ice sheets have been losing mass at an accelerating pace since 1992. Arctic sea ice has steadily declined since 1979 by 3.5-4.1% per decade. Between 1901 and 2010, global mean sea levels rose by 0.19 m, while ocean acidity increased by 26% (IPCC 2014). Some of these changes are occurring at an unprecedented pace and within greatly diminished, fragmented and degraded natural landscapes (Haddad et al. 2015, IPBES 2018), thereby severely challenging the ability of existing cultural and biological systems to adapt and persist.

Paleo-ecological studies have demonstrated that in the past, changes comparable in scale and magnitude to those projected for the latter half of the 21st century have resulted in major ecological upheavals, including biome shifts, extensive reorganization of communities, displacement of species and even large-scale extinctions (MacDonald et al. 2008, Gill et al. 2009, Woodburne et al. 2009, Jaramillo et al. 2010).

Shifting Ranges and Extinction Risk

There is conclusive evidence that ongoing climate change is having an impact on biodiversity globally. Changes in temperature, precipitation and other abiotic parameters associated with climate (e.g. increased CO_2 or sea level rise), are affecting individuals, species and communities in many complex ways (Bellard et al. 2012; Settele et al. 2014). Several species are shifting their ranges upslope and poleward in response to higher temperatures (Parmesan and Yohe 2003, Chen et al. 2011, references in Weins 2016). In India, upslope range shifts have been noted for several montane bird species but the extent to which these can be attributed to climate change is not known (Robin this volume). Range shifts (27.53 ± 22.04 m/decade) have also been reported for endemic Himalayan plants (Telwala et al. 2013). Poleward range expansions have been observed in the commercially important oil sardine (*Sardinella longiceps*) (Namboothri et al. this volume) and a few freshwater fish (Bhat this volume).

Interactions between the impacts of changing temperature, precipitation and land use have also led to downslope or non-poleward range shifts (Tingley et al. 2012; Settele et al. 2014). There is a large variation in observed species' range responses, both across and within taxonomic groups (Chen et al. 2011). In general, butterflies are better able to track changes compared to birds, while many plants and freshwater fish appear to be lagging behind, with range contractions being noted in the case of some cold-water fish (Settele et al. 2014). Despite the complexity in species' responses, it is clear that some groups (e.g. insects and birds) have shifted their ranges substantially in response to climate change (Settele et al. 2014).


Photo: Sameer Jain

A global analysis based on current and projected future climate velocity (i.e., the rate of change in temperature over time divided by the rate of change over distance) and average dispersal rates of taxonomic groups indicates that herbaceous plants and many trees are unlikely to keep pace with projected rates of future warming, except possibly in mountainous areas where climate velocity is lower (Settele et al. 2014). Several primates are at risk as they occur in lowland habitats that have high climate velocity. Other groups vulnerable to very high rates of future climate change (>0.06°C yr^{-1}) include rodents, some carnivores and freshwater molluscs (Settele et al. 2014). Many species will be unable to track suitable climates at the highest rates of projected future climate change (for the end of the 21st century), while most species would be able to do so at the low end of projected future change (Settele et al. 2014). The analysis highlights the importance of minimizing future increase in temperature, as well as the importance of mountainous areas, especially for the preservation of species with low displacement capacity.

Species' responses such as range shifts are difficult to model and predict as they are mediated by several interacting external (e.g. temperature and rainfall shifts and other global change factors), as well as endogenous factors (e.g. genetic, phenotypic, life history, interspecific interactions, dispersal and colonization ability) (Tingley et al. 2012, Sundaram et al. this volume). The mechanisms behind range shifts include changes in abundance – through increased mortality, emigration or altered recruitment – leading to increases at the 'cold edge' or local extinctions at the 'warm edge' of species' ranges (Wiens 2016). A global analysis found widespread (47% of 976 species surveyed) evidence of local extinctions due to recent climate change (Wiens 2016). Local extinctions were significantly more common in tropical and freshwater habitats and among animals (especially fish and insects), when compared to plants (Wiens 2016). This finding is significant, as it indicates failure of some populations to adapt to the relatively slight degree of climate change that has already occurred. It reinforces the importance of range shifts as a coping mechanism and highlights the risk to species with low dispersal ability and communities restricted to mountaintops, cold-water habitats, islands and peninsulas (Vijayakumar; Kunte this volume), as they literally have nowhere to go.

While habitat loss and degradation continue to be the main factor driving extinction risk in the 21st century (IPBES 2018), the scientific consensus is that the worst-case projections for future climate change will increase global extinction risks for many species – these species will be unable to adapt or track suitable habitat (Settele et al. 2014). Model-based projections for proportion of species facing elevated extinction risk range from <1% to >50% of the species studied. While there is a lack of clarity and consensus on the number of species facing increased extinction risk from the changing climate and the time it will take for them to go extinct (Settele et al. 2014), the risk of extinction remains a significant issue that needs to be addressed.


Photo: Arundhati Das

Physiological and Behavioural Responses

Besides shifting their ranges, species could also respond to climate change through changes in physiology and behaviour as well as changes in phenology (Bellard et al. 2012). These changes could be brought about by short-term plasticity in traits or by micro-evolution (Bellard et al. 2012).

Thaker and Batabyal (this volume) indicate how studying biodiversity in urban areas – where higher temperature and novel biotic and abiotic contexts exert unprecedented selection pressure on species – could provide insights into the interactive and complex responses that future climate change could trigger. These responses would occur at multiple levels of organization, from the physiology, behaviour and phenology of individuals to changes in population structure and interspecific interactions. There is evidence from urban areas of behavioural and physiological plasticity across individuals in new environments. This could provide insights into which species might adapt best to climate change in natural landscapes as well.

Tropical ectotherms (reptiles, amphibians, fish and insects) may be particularly vulnerable to climate change, as they have evolved in environments with relatively constant


Photo: Arundhati Das

temperature. These species exist closer to their upper thermal limits and have limited acclimation abilities and behavioural flexibility (Tewksbury et al. 2008, Deutsch et al. 2008, Sunday et al. 2014). Most ectotherms use adaptive behavioural mechanisms to avoid overheating, especially in tropical lowlands. Tropical forest ectotherms may be particularly at risk as they are adapted to shady environments and have limited behavioural options to evade warming (Tewksbury et al. 2008). The availability of cool microhabitats, behavioural flexibility and fitness costs of thermal retreat are important determinants of ectotherm sensitivity to climate change (Sunday et al. 2014). Behavioural plasticity can allow ectotherms to adapt to climate change up to a certain degree. Beyond this, species that can rapidly evolve greater thermal tolerance will have greater probability of long-term survival (Bellard et al. 2012, Thaker and Batabyal this volume).

Among aquatic ectotherms, warming could lead to increased selection for smaller body size, both at the individual and community levels, as it is associated with rapid turnover and low investment. Recent spawning declines have been noted for commercial fish species in the Gangetic plains, possibly caused by increasing water temperature. There have also been shifts from seasonal to year-round spawning in other species important for artisanal fisheries (see Krishnaswamy et al. this volume). Increasing salinity and temperature in the Sundarbans are altering reproductive behaviour and distributions of some commercially important species (e.g. Pabda (*Ompok pabda*), Tangra (*Mystus gulio*), *Notopterus* spp.; Bhat this volume). In general, climate change is expected to aggravate and magnify the existing selective pressures exerted by fisheries, causing further trophic declines and reduction in body size.

Among reptiles, turtles and crocodilians are especially sensitive to both gradual and sudden changes in temperature and precipitation. Nest temperature in these groups determines the sex of the hatchlings, and therefore increasing nest temperatures would have a direct impact on population sex ratio and recruitment success (Krishnaswamy et al.; Shanker this volume). The critically endangered gharial (*Gavialis gangeticus*) nests in sand banks, and altered flood regimes and warming nest temperatures might affect nesting success or cause further population decline by altering sex ratios among hatchlings (Krishnaswamy et al. this volume). Amphibians are extremely sensitive to climate change, owing to their physiological dependence on temperature and precipitation cues at every stage of their life cycles. They are also the group most severely threatened by other global change factors and the spread of chytrid fungus. However, there is little to no research on how climate change is impacting amphibians in India. A few studies indicate that endemic frog species in the Western Ghats and Himalaya may suffer habitat loss and range shifts under future climate change (Krishnaswamy et al.; Vijayakumar this volume).

Wildlife-human conflict is a major conservation challenge in the Indian context. Changes in movement and behaviour of elephants and lions have been observed following severe droughts triggered by El Niño events (Sukumar this volume). Owing to multiple environmental and climatic factors, elephants have migrated to regions where they had not been seen for hundreds of years, resulting in multiple casualties when they crossed paths with humans who were not used to them. Similarly, drought triggered an increase in human-lion conflict in Gir Forest, leading to human deaths again. It is speculated that climate change may exacerbate such conflict with wildlife. However, very little research has been done on this topic (Sukumar this volume).

Phenological Responses and Altered Interspecific Interactions

One of the most visible and well-documented responses to climate change is the shift in the timing of life cycle events in plants and animals. As discussed above, the breeding times of many fish and reptiles are shifting. Changes have also been noted in birds and insects (Peñuelas et al. 2013, Settele et al. 2014). Insects in temperate regions have longer summer activity periods, more breeding cycles and larger larvae (see references in Peñuelas et al. 2013). Several Northern Hemisphere birds and amphibians show earlier breeding and oviposition in response to warming (Peñuelas et al. 2013). Egg-laying dates have advanced by approximately 4 days per decade (Parmesan 2007). Bird migration patterns are also changing (Quader this volume), with spring migrants arriving earlier by 1.3-4.4 days per decade in Europe and North America (Walther et al. 2002). The shift in early arrival appears greater for short-distance migrants compared to long-distance ones (Settele et al. 2014).
The advancement of spring phenology in response to warming is particularly apparent in high-latitude and high altitude plant species (Settele et al. 2014). Shreshta et al. (2012) estimate that on average, the start of the growing season in the Himalayas has advanced by 4.7 days, with an increase in the length of growing season by the same amount.

Phenological responses in tropical plants are less well-studied. The phenology of many tropical trees is strongly influenced by duration of solar irradiance and seasonality in rainfall, specifically, the effects of duration and intensity of precipitation on soil moisture availability and water stress (Ramaswami et al. this volume and references therein). There is strong seasonality in vegetative phenology in seasonally dry tropical forests. Leaf flush across most tree species in dry deciduous forests in southern India has been shown to peak two months before the peak of the summer monsoon (Murali and Sukumar 1993). Similar seasonal patterns are reported from other forest types across India (Ramaswami et al. this volume). In general, leaf production and growth appear to be positively correlated with seasonal rainfall.

Flowering closely follows or coincides with leaf fall, while fruiting predominantly occurs during the wet season (Ramaswami et al. this volume). Flowering of wind-dispersed trees in a semi-evergreen forest in north-eastern India was found to be inversely related to rainfall and minimum temperature, as was fruiting. Flowering of bird-dispersed species did not show such patterns, and fruiting of such species was positively correlated with rainfall amount and duration. In a semi-arid tropical scrubland in southern India, the onset of reproductive and vegetative phenophases in shrubs was correlated with early summer showers and appear to be triggered by a reduction in moisture stress (Ramaswami et al. this volume).

Plant phenology is influenced by short-term weather phenomenon such as the El Niño Southern Oscillation (ENSO), as well as by ongoing longer-term changes in temperature and rainfall (Detto et al. 2018). Hence long-term observations are necessary to detect and attribute phenological shifts in response to climate change. Ramaswami et al. (this volume) find that most phenological studies in India last for only two years. The short duration of studies is therefore a major impediment to our ability to understand the impacts of climate change on plant phenology in India and the downstream consequences of climate-driven phenological shifts. Another challenge is that tropical plant phenology is driven more directly by seasonality and amount of precipitation rather than temperature. There are still large uncertainties in model projections for future changes in rainfall. It is also not known how ENSO would be affected by climate change (IPCC 2013).

Phenological shifts in plant resources would affect all higher trophic levels in ecosystems. The phenology of insect herbivores, pollinators and frugivores is closely synchronized to that of plants (Murali and Sukumar 1993, Devy et al.; Ramaswami et al. this volume), particularly so for mutualists such as the fig wasp (Devy et al. this volume). Breeding times of insectivorous birds are linked to the emergence and abundance of prey species (Both et al. 2010). Shifts in phenology are also likely to increase interspecific competition among plants (e.g. canopy vs. understorey species) and invertebrates (Peñuelas et al. 2013). Advanced reproductive period in mid and late-season grasshopper species in Mongolia led to overlaps with early-season species, increasing interspecific competition (Guo et al. 2009).

Apart from inducing phenological mismatches, warming and drought directly affect abundances of insect pollinators (Peñuelas et al. 2013), which in turn would affect fruit set and maturation (Devy et al. this volume). This is likely to have consequences for the food availability and breeding cycles of several avian frugivores, especially in evergreen and semi-evergreen tropical forests (Ramaswami et al. this volume, Ganesh and Davidar 2001).

Recent studies indicate that altered interspecific interactions could be a stronger driver of climate-related changes in abundance and local extinctions than species' physiological tolerance. Such interactions may therefore play an important role in mediating species' ability to persist under future climate change (Settele et al. 2014).

Ecosystem Functions and Services


Photo: Prasenjeet Yadav

Ecosystems serve every kind of human need, providing food, fuel, fibre and water. They regulate the spread of pests and diseases, and the impact of natural hazards such as flooding. They contribute to human livelihoods and well-being in other fundamental ways by recycling nutrients, storing carbon, regulating climate and maintaining the hydrological cycle. Finally, humans derive great cultural and psychological benefits from the natural world (Millennium Ecosystem Assessment 2005), and food production depends on nutrient cycling by soil biota, as well as on successful pollination and the regulation of pests. Osuri et al. (this volume) discuss how the flow of ecosystem services depends upon ecosystem functions, which in turn derive from processes and interactions across all scales of biological organization from the individual to the biome. They present a conceptual model of the possible mechanistic pathways through which climate change could affect ecosystem services and interact with existing human exploitation of ecosystems to create negative feedbacks. In this model, climate impacts could occur through direct or abiotic pathways such as increases in stream flow resulting from higher rainfall. They could also occur through more indirect, gradual impacts on individual organisms that then scale up to affect ecosystem functions.

Ecosystem functions are impaired by the loss of species as this leads to reduced co-occurrence of interacting species (Burkle et al. 2013), and often, these services are affected long before species actually go extinct (Valiente-Banuet et al. 2015). This is especially true when keystone species (e.g. pollinators) or disease vectors shift their ranges or undergo changes in abundance, via local extinctions and colonization. Regulation services depend greatly on established interspecific interactions (e.g. plant-pollinator, predator-prey or host-pathogen), and as ecological communities change in response to global change drivers, shifts in these interactions will occur, which may reduce the effectiveness of these services (Settele et al. 2014, Osuri et al. 2016, Devy et al. this volume).

Current knowledge on the relative magnitude of these various effects in the Indian context is sparse. However, this is changing rapidly, as there has been more than a ten-fold increase in the rate of publication on climate change and ecosystem services in India in the past 3 years (Osuri et al. this volume). The model presented by Osuri et al. (this volume) provides a framework for essential future research into quantifying the links between climate change impacts and ecosystem services.

Vulnerability of Major Habitat Realms to Climate Change

Tropical Forests

Tropical forests hold much of the earth's biodiversity as well as more than half of the world's forest carbon stocks (Pan et al. 2011). Their role in the sequestration of


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carbon dioxide is critical to the regulation of the earth's climate and in mitigating the effects of anthropogenic greenhouse gas (GHG) emissions. There is, however, considerable uncertainty regarding their sustained ability to act as carbon sinks – given the rapid and widespread degradation and loss of tropical forests worldwide (Baccini et al. 2017) and the interaction between the impacts of climate change and other global change factors (Settele et al. 2014; Brienen et al. 2015). In India, hundreds of millions of people are directly dependent on forests for fuelwood, grazing and non-timber forest products (Osuri et al. this volume).

Long-term forest studies in India indicate that the dynamics of seasonally dry tropical forests vary at decadal time-scales and are influenced to a large degree by the amount and seasonality of rainfall. The spatio-temporal variation in precipitation pattern affects community composition, species diversity, tree demography, phenology, patterns of growth, fire regimes and the spread of invasive species in these forests (Das and Sukumar; Ramaswami et al. this volume). The dynamics of tropical dry deciduous forests in particular are more sensitive to stochasticity in climatic factors (especially rainfall, owing largely to its modulation of the frequency and intensity of fire) and the species-specific effects of prolonged drought (Das and Sukumar this volume and references therein).

Climate change-driven alteration of precipitation patterns and possible increased frequency of drought would therefore have profound implications for dry deciduous forests in India and consequently, the ecosystem services they provide. Long-term studies from other tropical forests show that increases in temperature could affect rates of photosynthesis, patterns of carbon allocation, tree growth and mortality (Settele et al. 2014; Anderson-Teixeira et al. 2015). Modelling studies on the exposure and vulnerability of Indian forests to future climate change indicate that more than a third of forested habitats are likely to experience severe impacts, with the drier and more temperate forest types (particularly in northern, central and south-eastern India), and western Himalaya being most at risk of transitioning from the existing forest type to another (Rasquinha and Sankaran 2016; Sharma et al. 2017).

The pathway through which invasive species establish themselves is also likely to be affected by the changing climate, and local people whose livelihoods are dependent on forests for sustenance could be adversely affected by the combined impacts of climate change and invasive species (Sundaram et al. this volume). However, the authors note that in some cases, people have come to rely on these very species – for example, artisanal communities generate income by using *Lantana*.

Coastal and Marine Ecosystems

Coastal and marine habitats are being affected by climate change in multiple ways, including increase in sea surface temperatures (SSTs), sea level rise, increasing frequency of extreme weather, changing circulation patterns and increased ocean acidification (Namboothri et al. this volume). Between 1961 and 2005, average SSTs increased by 0.2°C along most of the Indian coastline, and by 0.3°C along the south-eastern coast. Increasing temperatures are affecting the distribution of fish species, including those that are important for commercial fisheries (e.g. sardines). Over 4 million people depend directly on the sea for their livelihoods with three times as many dependent on the associated economy (Namboothri et al. this volume and references therein). Sea-level rise along the Indian coastline has been consistent with the global average (1.29 mm yr^{-1}). Approximately 250 million people, living within 50 km of the coast, could be affected by these changes. The risk is particularly high for regions with low-lying coastlines such as the Ganges-Brahmaputra delta, and the Lakshadweep Islands, as these areas are simultaneously affected by rapidly submerging coastlines and increased storm surges from cyclonic events (Namboothri et al. this volume and references therein). Coastal habitats such as mangroves are already threatened by developmental activities and changes in sedimentation patterns, which could affect their ability to respond to climate-induced changes (Bhat; Namboothri et al. this volume).


Photo: Adhith Swaminathan

Coral reefs are among the most biodiverse systems on the planet. The ecosystem services provided by reefs support the livelihood of millions through tourism, fishing and coastal protection (Namboothri et al. this volume). It is estimated that between 25-30% of all marine species have some part of their life cycle in coral reefs (Wright and Watson 2018). In the past two decades, coral reefs in the Andaman and Lakshadweep Islands have been hit by multiple ENSO-linked bleaching events, resulting in reduced coral cover. (Namboothri et al. this volume). As global bleaching events become more frequent, the ability of coral reefs to recover is being compromised by other factors such as stronger storm surges, coastal development, increased sediment run-off, sewage discharge, eutrophication, overfishing and coral mining. This is resulting in declines in both coral cover and species diversity, which in turn is further suppressing their ability to recover from successive disturbances (Namboothri et al. this volume).

Himalaya

The Himalaya is one of the regions that is most vulnerable to climate change (Xu et al. 2009). Temperature is increasing more rapidly in this region compared to others. A seasonal increase of about 2°C in mean temperature was reported between 1984 and 2007 in the Western Himalaya (Shekhar 2010 cited in Naidu et al. this volume). Naidu


Photo: Vikram Sathyanathan

et al. (this volume) find that between 2001 and 2015, winter temperatures decreased in the southern regions of the Western Himalaya, while growing season temperatures have increased. During the same period, the Eastern Himalaya showed warming throughout the year, while there was a decline in winter precipitation in the Sikkim Himalaya.

The Greater Himalaya is the source of ten of the largest Asian rivers, and the mountain range has a profound impact on the Indian monsoon. Changes in snow and ice melt could result in excessive or insufficient water supplies over short and long terms. Immerzeel et al. (2010) predict a reduction in freshwater availability over the next 30 years in the Indus and Brahmaputra basins. Corlett and Lafrankie, Jr. (1998) predict that changes in plant phenology, due to rising temperatures, would have serious consequences for both plants and animals. Phenological observations from the region have reported both delays and advances in flowering in response to winter temperatures (Naidu et al. this volume and references therein). There have been changes in the length of the growing season, including earlier onset, as a result of temperature and precipitation patterns (Shrestha et al. 2012, Naidu et al. this volume).

High sensitivity to climate change and long recovery time from disturbances place alpine and subalpine species at great risk (Bawa et al. 2010). The loss of key species in alpine ecosystems could trigger secondary extinctions (Xu et al. 2009). The effects of climate change could exacerbate the problems caused to snow leopards (listed as vulnerable species by IUCN) from habitat loss (Forrest et al. 2012). Studies predict a loss of about 40% of forest cover in the Himalayan region during the 21st century, particularly in the Western Himalaya (Pandit 2007). Himalayan forests hold water and soil, regulate climate, host a diverse number of species, act as carbon sinks, and control stream flow, besides providing livelihoods for local people (Xu et al. 2009). In some parts of the arid regions, warming is linked to desertification caused by increased snowmelt and reduced plant productivity. This has implications for grasslands and livestock grazing (Naidu et al. this volume). Local communities are therefore particularly vulnerable to major transformations of Himalayan ecosystems (Naidu et al. this volume).

Freshwater Ecosystems

Freshwater habitats in India are under severe threat from anthropogenic factors such as water abstraction, pollution and large-scale transformation of wetlands, rivers and streams. These systems have been so manipulated and overharvested, that the impacts of climate change can only be understood in the context of their interaction with other anthropogenic impacts (Krishnaswamy et al. this volume).

There is general agreement that climate change will increase air and water temperatures in freshwater systems and alter the rate and timing of flows (Bhat, this volume). However, predictions for the effects of changes in precipitation and runoff responses vary widely (Krishnaswamy et al. this volume). Globally, riverine habitats are predicted to experience an increased frequency of rainfall extremes, short-term increases in flooding followed by prolonged droughts, and decreases in dry-season river flows (Bhat; Krishnaswamy et al. this volume and references therein). Increased salinisation of rivers due to sea level rise would impact water and food resources for densely populated regions (Osuri et al. this volume).

Accelerated snowmelt in the Himalayas is probably contributing to heightened springtime dry season flows, affecting the onset of flooding as well as increasing flood risk in the Indus-Ganga-Brahmaputra basins (Krishnaswamy et al. this volume and references therein). The general weakening of the summer monsoon and increase in extreme rainfall events, especially over central India, will affect river flows in a region where most rivers are highly regulated and water is diverted for irrigation. This in turn will directly affect flooding regimes and the ability of riverine organisms to adapt to changing climate (Krishnaswamy et al. and references therein, this volume).

Freshwater habitats have the greatest proportion of threatened species (Settele et al. 2014), and climate change could further aggravate threats to freshwater organisms by altering environmental cues that species depend on to breed and disperse (Bhat, this volume). It could also directly affect species' biology (e.g. by increasing thermal adaptation or through sex determination). The degree of risk is likely to be specific to life stage for larger vertebrates and to vary across life history traits, behavioural plasticity, and phylogenetic history of species (Krishnaswamy et al. and references therein). Krishnaswamy et al. (this volume) present a conceptual framework for studying impacts of climate change on freshwater biodiversity in human-dominated riverscapes. Such frameworks can be used to construct testable hypotheses and guide further research. They caution that hydropower regulation of rivers is a more immediate threat, requiring urgent management action, compared to future climate change.

Looking Forward

Under a moderate emissions scenario (IPCC 2014), India is projected to experience 1-2°C of warming by 2030, and 2-3°C by the end of the century, compared to the 1961 – 1990 baseline (Chaturvedi et al. 2012). The Himalaya and north-western regions in particular will experience greater warming under this scenario (2-3°C by 2030 and up to 5°C by the end of 21st century). Temperature could rise by 5°C for most of the country (with Himalayan warming approaching 7°C) (Chaturvedi et al. 2012) under the most extreme emissions scenario (IPCC 2014). Precipitation is predicted to increase by 6-14% later this century (Chaturvedi et al. 2012), with an increase in inter-annual variability and more frequent extreme rainfall during the summer monsoon (Christensen et al. 2013). However, model predictions for future changes in rainfall are more variable and quite uncertain compared to those for temperature (IPCC 2013).

Much of India's population depends heavily on the resources and services that ecosystems provide, and studies have shown that there are likely to be severe adverse effects of climate change on human health, living standards and productivity (Im et al. 2017; Muthukumara et al. 2018). Central Indian states are likely to be most severely affected with possible reductions in income of up to 9.8%. The cost of inaction in terms of total GDP losses for India has been estimated at about 1,178 billion USD by 2050 (Muthukumara et al. 2018). Therefore, there is an urgent need for the implementation of policy and management initiatives that integrate climate change mitigation and adaptation with developmental planning (Seidler and Bawa 2016), and conserve ecosystems which play a fundamental role in facilitating mitigation and adaptation.

Across chapters in this report, it is agreed that habitat loss and degradation remain the major drivers of biodiversity loss and must be addressed on an urgent basis, in light of the threats posed by future climate change. The immediate effects of certain types of existing human use and pressure on natural systems must be managed and mitigated as they can undermine ecosystems' ability to adapt to and recover from climate-induced changes, with knock-on effects for human livelihoods and health (Namboothri et al.; Sundaram et al. this volume). This is particu-

Topic	Knowledge Gaps	Significance
Ecosystem services	• Climate effects on supply of NTFPs • Role of ecosystems in buffering disease outbreak • Climate change (CC) impacts on carbon and nutrient cycling and activity of soil microbes • Effect of drought on carbon sequestration potential • Interactions between CC and other global change factors	• Rural livelihoods • Human health • Supporting national commitments on climate mitigation • Mitigating CC • Livelihoods, human health, mitigation of future CC
Phenology and pollination	• Trophic consequences of phenological mismatch • Ecosystem-level changes in phenological patterns	• Ecosystem services (pollination) • Ecosystem services (NTFPs)
Long-term forest dynamics	• Long-term forest dynamics studies across multiple spatial scales in all major forest types • Effects of elevated CO_2 on tree growth • Interaction between CC impacts and habitat degradation and nutrient deposition	• Ecosystem services (livelihoods, C sequestration) • Mitigation of CC • Ecosystem services (C storage), mitigation of CC • Ecosystem services (C storage), mitigation of CC
Freshwater and marine ecosystems	• Vulnerability of biodiversity to CC • Interactions between CC impacts and other human-induced changes • Effects of ocean acidification	• Conservation, management of aquatic species and adaptation to CC • Ecosystem services (livelihoods, human health)
Montane ecosystems	• Biophysical dynamics of Himalaya • Vulnerability of biodiversity to CC • Adaptation of local communities to CC	• Management and conservation of biodiversity, mitigation of CC • Livelihoods, human health, development
Urban ecosystems	• Mechanisms behind phenotypic changes in species and populations in response to CC • Fitness consequences of species phenotypic and functional response to CC and urbanisation	• Conservation, management of urban species and mitigation of CC • Conservation, management of urban species and mitigation of CC
Invasive species	• Mechanisms behind invasive ability • Impacts of invasion on ecosystem dynamics • Distributions and changes in distribution of invasives	• Management of invasives, restoration • Ecosystem services (livelihoods, nutrient cycling) • Management and conservation of biodiversity
Wildlife-human conflict	• Impacts of CC on movement and habitat use of conflict-prone species • Incentives for maintaining biodiversity-friendly land-use	• Wildlife management, conflict mitigation, livelihood protection • Livelihoods, conflict mitigation

Table 1. Critical knowledge gaps and areas for further research specifically identified by authors

larly true in the case of unplanned development linked to urbanisation, infrastructure development and extractive industries. Such activities, along with the expansion of croplands, agroforestry-related activities and spread of invasive species, cause significant habitat degradation in South Asia, leading to widespread losses of biodiversity and ecosystem services (IPBES 2018). The authors also agree that there are critical knowledge gaps (Table 1) that must be filled in order to effectively conserve biodiversity in the face of climate change. This issue is addressed in detail in the following sections.

Need for Further Research

Species and communities are expected to experience and respond to climate change idiosyncratically (Root et al. 2003). At present, there are immense knowledge gaps with regard to the exposure, sensitivity and adaptive capacity (sensu Dawson et al. 2011) of the vast majority of Indian species and ecosystems to climate change. Unfortunately, some of the most sensitive taxonomic groups such as amphibians, butterflies and freshwater molluscs, which have high rates of endemism, are the most data deficient (Vijayakumar; Kunte; Krishnaswamy et al. this volume). There is a lack of continuous, widely accessible long-term (>20 years) or baseline datasets, (Ramaswami et al.; Namboothri et al. this volume) and the strong, confounding presence of other anthropogenic influences such as resource extraction, habitat loss and degradation. Finally, there is very little research on the degree to which species are able to evolve adaptations to ongoing and future climate change.

Recent modelling studies have attempted to assess the exposure of certain endemic plants (Priti et al. 2016; Sen et al. 2016) and vertebrate species (Sony et al. 2018) to climate change, as well as entire biomes and habitat types (Rasquinha and Sankaran 2016; Sharma et al. 2017). However, there is an urgent need for collaborative projects that adopt a complementary suite of methodological approaches to understand the mechanisms behind species and ecosystem responses to global change in the Indian context. Such approaches include long-term observational studies, mechanistic modelling, as well as experimental or manipulative studies that simulate future climate conditions in laboratory as well as field settings (Dawson et al. 2011; Peñuelas et al. 2013).

Need for Long-Term Monitoring and Compiling Baseline Data

The complexity at every level of organization – from individuals to biomes – and the inherent stochasticity of natural systems, lead to considerable uncertainty in our ability to predict how these entities will respond to climate change. Long-term monitoring networks in other parts of the tropics have been very effective in understanding how tropical communities are responding to global change and potential future changes, and consequent implications for carbon sequestration (Brienen et al. 2015; Esquivel-Muelbert et al. 2018). Existing long-term monitoring efforts demonstrate that it is necessary to monitor ecosystem dynamics at decadal time-scales before climate change-driven impacts can be detected (Anderson-Teixeira et al. 2015). A representative long-term monitoring network could alert us to climate-driven directional changes in ecosystems and improve our ability to prepare for impending losses or drastic reorganization of natural communities that are important for human well-being.

The MoEFCC has proposed the establishment of a network of Long-Term Ecological Observatories (LTEO-India) as part of the Climate Change Action Programme of India (MoEFCC 2015). This network would cover major biomes in India and aid in understanding the various anthropogenic and biophysical drivers that result in ecosystem change, while considering social and ecological perspectives. Here we suggest that species, communities and ecosystem functions (e.g. pollination) that show high sensitivity to climatic factors be identified as research priorities within the proposed sites. Finally, existing and recently established long-term studies (Devy et al.; Ramaswami et al.; Das and Sukumar this volume) should be supported so that their continuation is ensured.

In addition to long-term studies, several authors have highlighted the value of citizen science initiatives in providing coarse-scale information on spatiotemporal trends in species' distribution (Sundaram et al. this volume) and phenology (Ramaswami et al.; Quader this volume). Efforts could be made to integrate such initiatives with long-term monitoring studies, which are more intensive and site-specific. Finally, data from early studies on tree growth and mortality (conducted by institutions like the Indian Council for Forestry Research and Education and State Forest Research Institutes) could be made more accessible to the scientific community (Tewari et al. 2014), as they can provide valuable baseline data. Such sites, for which baseline data exists, should also be re-surveyed to investigate changes.

Recommendations for Management and Conservation

The effective management and conservation of biodiversity is a prudent way of ensuring that climate change mitigation goals are met, and that local communities are able to adapt to future climates with minimal disruption in the flows of ecosystem services. Conservation approaches need to be inclusive and adaptive to ensure benefits for (often marginalised) local communities, and to cope with dynamic social-ecological systems (Shanker et al. 2017). As the livelihoods of most rural communities are closely linked to natural resources, they often provide the best knowledge on how climate change is impacting ecosystems which they are a part of (Bawa et al. 2010). Efforts must be made to integrate such knowledge into management and planning. Thus, the support and involvement of local communities are essential for effective future management.

The protected area (PA) network in India is composed of relatively small, often isolated reserves (Rodgers et al. 2002). An assessment of the vulnerability of the current PA network to climate change would help identify PAs that should be targeted for mitigation and adaptive measures, including extending buffer zones and providing incentives for biodiversity-friendly management of land


Photo: Prasenjeet Yadav

adjoining PAs (Sukumar this volume). Ensuring connectivity of habitats and removing barriers to dispersal of species is especially important in flat, low-lying regions where species will have to move greater distances to track suitable habitats (Settele et al. 2014). In mountainous areas, connectivity of reserves should be oriented along elevational gradients to facilitate upslope movement of species in response to warming (Halpin 1997). Strategic afforestation and restoration of abandoned agricultural lands should be undertaken to improve habitat connectivity and mitigate the effects of climate change (Naidu et al. this volume). Maximizing species diversity in agroforestry systems and farmlands would help sustain the flow of ecosystem services such as pollination (Devy et al. this volume) and pest control, while also allowing for sufficiently heterogenous landscape mosaics that could facilitate the dispersal of wild species.

Finally, coordinated landscape-scale planning and zonation is an important step towards achieving climate change mitigation and adaptation goals, in addition to biodiversity conservation and sustainable development ones (IPBES 2018). Various competing sectoral interests and needs (e.g. agriculture, biodiversity, urban and infrastructure, resource extraction, etc.) must be systematically considered in light of the need to mitigate and adapt to future climate change. Land use planning and zoning decisions can then be taken to optimise efficiency in meeting sectoral needs, while also sustaining natural ecosystems and the services they provide. This would also help reduce impacts of non-climate stressors on ecosystems. However, care should be taken to ensure that land use policies aimed at climate change mitigation do not negatively impact biodiversity in ecologically sensitive regions (Jantz et al. 2015).

Conclusion

At the current rate of warming, global temperatures are projected to increase by 1.5°C above pre-industrial levels in the next two decades (IPCC 2018). There is mounting evidence that the scientific community has underestimated the sensitivity of earth's ecosystems to small increases in temperature, and the consensus is that efforts must be made now to limit warming to 1.5°C instead of 2°C (IPCC 2018; Resplandy et al. 2018).

While there has been a large increase in climate change-related research in the last decade, particularly with regard to ecosystem services, critical knowledge gaps remain. There is a need for long-term monitoring and studies assessing the vulnerability of biodiversity to climate change, particularly in central, north-eastern and north-western Indian biomes, and in montane habitats, dry forests, xeric habitats and freshwater and marine ecosystems. Such studies would help inform better ecosystem management in order to mitigate the effects of climate change and facilitate adaptation for local communities by conserving the ecosystem services they depend on for their health, livelihoods and well-being.

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Climate Change Impacts on Ecosystem Functions and Services in India: An Exploration Of Concepts and a State of Knowledge Synthesis

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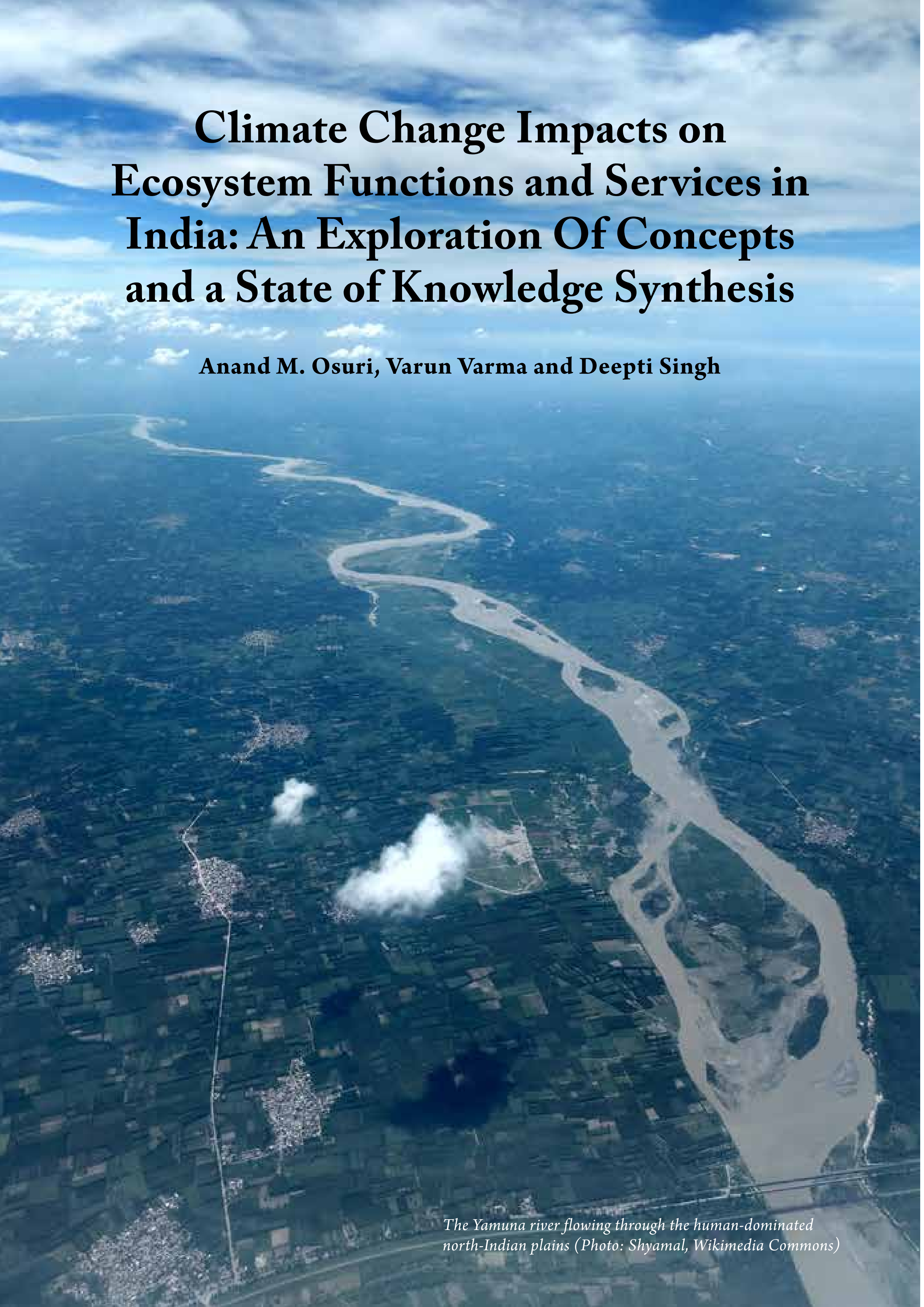


The Yamuna river flowing through the human-dominated north-Indian plains (Photo: Shyamal, Wikimedia Commons)

Introduction

The rapid escalation of human impacts on the global environment over the last 400 years has led scientists to define a new period in Earth's geological history – the Anthropocene epoch (Cruzen 2002). This new epoch is distinguished from its predecessor, the Holocene, by the substantially higher influence of humans on major biogeochemical processes on land, in the oceans and in the atmosphere (Lewis and Maslin 2015). For example, concentrations of nitrogen on land and carbon in the atmosphere are substantially higher at present than at any time over the last million years, if not longer (Lewis and Maslin 2015). One of the defining features of the Anthropocene is the ongoing change in the earth's climate, driven in large part by the accumulation of carbon dioxide and other heat-trapping greenhouse gases in the atmosphere at an unprecedented rate due to industrial activity, burning of fossil fuels and deforestation (IPCC 2014). Climate change is most widely recognised as increasing global land and sea temperatures, changing precipitation patterns, and a rising frequency of extreme events such as heat waves, intense rainfall events, and droughts (IPCC 2018).

A changing climate can, in turn, have feedbacks that affect the environment, and interactions between humans and the environment. For example, the melting of ice reserves at high latitudes due to global warming, and changes in major ocean currents, are driving an increase in global sea levels (an estimated 4 cm increase during 1993-2010) that threaten coastal ecosystems as well as the livelihoods and well-being of humans in densely populated coastal areas (IPCC 2014). The anticipated mass migration of humans away from coasts, and conflicts that could potentially arise due to such large-scale migration, are cause for growing concern (Smith 2007). Climate change can also affect the human-environment relationship by altering the supply of ecosystem services, or benefits that humans derive from natural ecosystems, such as food, water, fuel and raw materials (Mooney et al. 2009). It can do so by driving changes in biological communities and biogeochemical processes in ways that alter the flow of services from these systems, with ecosystem services varying from one another in how they respond to climate change (Mooney et al. 2009).

Understanding the impacts of climate change on biodiversity, ecological functions and ecosystem services has emerged as a major priority area for research – since the year 2000, there have been at least 2100 papers on climate change and ecology in journals published by the Ecological Society of America (in contrast, the number of climate-related papers published before 2000 in these journals was 275).

In India, which comprises 11 major biomes or ecoregions according to the WWF classification (Olson and Dinerstein 1998), and hosts two global hotspots of biodiversity (Myers et al. 2000), a large fraction of the human population depends directly on benefits and resources derived from natural ecosystems such as fuelwood and non-timber forest products (Chopra 1993; Kataki and Konwer 2002). The drivers of India's major sources of surface and groundwater – namely, the monsoon cycle and snowmelt from the Himalaya mountains – are both sensitive to changes in climate (Narsimlu et al. 2013). It is also increasingly clear that the distribution and functioning of India's biomes are likely to change under an altered future climate, with arid and dry vegetation types being replaced by wetter forms (Ravindranath et al. 2006; Rasquinha and Sankaran 2016). Even if global mean temperature rise is capped at 1.5-2.0°C, South Asia is projected to be one of the hotspots for impacts across multiple sectors including water, food and the environment (Byers et al. 2018; IPCC 2018). Understanding the impacts of climate change on ecosystems and the supply of ecosystem services in India is therefore essential for the formulation of effective climate adaptation and mitigation strategies.

This chapter provides an India-focused overview of climate change and its impacts on ecosystem services. Our report follows two broad themes. The first part has a conceptual focus and draws widely from international literature to define broad and sometimes contentious terms such as 'climate change' and 'ecosystem service' within the scope of this review. In this section, we also develop a simple conceptual model of the mechanisms that underlie climate change impacts on ecosystem services, and elucidate these mechanisms using examples from, or that are relevant to, the Indian context. The second part comprises a literature review that aims to establish the current state of knowledge pertaining to climate change and its impacts on ecosystem services in India. Using systematic searches of the peer-reviewed national and international literature, we aim to describe the volume and main focal areas of the literature on climate change and ecosystem services in India, and to summarise key insights into the threats posed by climate change to Indian ecosystems and services. We also attempt to identify important knowledge gaps and discuss priority areas for future research.

Climate Change and Indian Biomes

Climate change is expected to substantially modify future patterns of temperature and precipitation – these are the fundamental variables which determine the distribution of biomes around the world (IPCC 2018). Predictions for future conditions derived from general circulation models are organized as a set of scenarios, termed Representative Concentration Pathways (RCPs), which summarise changes in future emissions while assuming varying levels of social and technological mitigation of emissions (IPCC 2014). For example, RCP 2.6 represents the 'best case scenario' where substantial mitigation measures are implemented which will keep global temperature increases to within 2°C by the end of the 21st century, relative to pre-industrial temperatures. On the other hand, RCP 8.5 represents an extreme warming world, where no efforts are made to constrain emissions, leading to a 4-6°C increase in average global temperatures.

Averaged outputs from multiple general circulation models predict very consistent increases in temperatures for India by the end of the 21st century, relative to average conditions during a baseline period of 1986-2005. However, there is considerable spatial variation in the intensities across the country and for different emission scenarios. Under RCP 2.6, average temperature increases are expected to be 0 to 0.5°C for peninsular India and 0.5-1°C degree for central and northern India, as well as north-east India. If we consider RCP 8.5, temperature increases are likely to be 3-4°C for southern peninsular India and most of the north-east. Central and northern India will see temperature increases of 4-5°C, and the northernmost extremity of the country will possibly see a 5-7°C increase (IPCC 2014).

Precipitation over India is largely received from the monsoon, of which the south-west summer (June-September) monsoon contributes the vast majority of rainfall to most of the country, while the north-east winter (October-December) monsoon is the main source of rainfall for a few southern states.

Tropical dry forests and savannas, as those found along the eastern slopes of the Western Ghats, are expected to contract under future climate in India (Photo: AJT Johnsingh, WWF-India, NCF; Wikimedia Commons)

The regularity of the monsoon is critical for India's ecosystems, fresh water supply and economy, especially the agricultural sector. Hence, understanding the impact of climate change on the monsoon system – its intensity, as well as its spatial and temporal characteristics – is an important priority. Research thus far indicates that in a modified climate, the peak of the south-west monsoon could shift from the month of July to centre around August (Jena et al. 2016).

Analysis of observed data over the last 60 to 70 years demonstrates that there has been a decrease in frequencies of rainfall events classified as 'light', 'moderate' and 'rather heavy' (i.e. < 64.4 mm/day), coupled with increases in frequencies of events categorised as 'very heavy' and 'exceptionally heavy' (i.e. > 124.4 mm/day) (Pattanaik and Rajeevan 2010). In a separate analysis, Singh et al. (2014) demonstrated that short dry spell events have increased in frequency, but reduced in intensity, while wet spell frequencies have remained the same, but increased in intensity over central India during the peak summer monsoon season. Malik et al. (2016) further explored long-term trends in extreme dry and wet events during the same time period across different sub-regions in India and concluded that there are strong trends for intensified drought events for the north and north-west of India, as well as parts of peninsular India. There is also evidence of increased drought severity, duration, and frequency in central Maharashtra, coastal South India and the Indo-Gangetic Plains (Mallya et al. 2016). Central India and regions further east, on the other hand, showed increased likelihood of intense rainfall events that could suggest an increased propensity for floods (Roxy et al. 2017).

In terms of total seasonal precipitation, an aggregation of predictions from multiple GCMs suggests that under the RCP 2.6 scenario, precipitation could increase up to 10% across India, but will largely remain within bounds of natural variability. Under the more extreme RCP 8.5 scenario, a majority of the models suggest wetter conditions, with a likely 10-20% increase in precipitation across India. Additionally, some western, peninsular and north-eastern regions may see a 20-30% increase in precipitation (IPCC 2014). It is, however, important to note that the predictions for precipitation from these GCMs are less certain than predictions for temperature change, since a majority of the models are unable to accurately simulate the monsoon circulation features and their associated precipitation distribution (Ashfaq et al. 2017). Therefore, there remains considerable uncertainty in the predicted changes to the Indian monsoon rainfall characteristics.

Modification in temperature and precipitation regimes over India are likely to result in changes to the distribution of land-cover types and biomes in the country, and knock-on effects to the ecosystem services they provide humans. Rasquinha and Sankaran (2016) conclude from a modelling study that warmer and wetter average conditions over the country could result in substantial spatial reorganization of biomes. In all, their model predicts that under the RCP 8.5 scenario, approximately 18% of India's land mass could experience biome shifts, and that drier biomes – such as tropical dry forests, savannas and grasslands – as well as temperate biomes will be more susceptible to change. Figure 1 and Table 1 provide details on the extent and distribution of predicted changes under moderate (RCP 4.5) and severe (RCP 8.5) climate change scenarios, based on Rasquinha and Sankaran (2016).

Biome	RCP 4.5	RCP 8.5
Tropical and subtropical grasslands, savannas and shrublands	–73.62 (–83.52, –63.73)	–83.1 (–91.63, –74.56)
Rock and ice-covered areas	–71.79 (–76.14, –67.44)	–78.24 (–81.48, –75)
Tropical and subtropical coniferous forests	–33.1 (–39.51, –26.7)	–39.51 (–47.95, –31.07)
Temperate broadleaf and mixed forests	–15.7 (–24.28, –7.12)	–31.43 (–43.86, –19)
Deserts and xeric shrublands	–16.25 (–23.13, –9.37)	–28.78 (–40.83, –16.73)
Flooded grasslands and savannas	–14.61 (–20.78, –8.45)	–25.45 (–33.7, –17.2)
Temperate coniferous forests	–7.3 (–12.13, –2.48)	0.42 (–8.25, 9.1)
Tropical and subtropical dry broadleaf forests	7.28 (4, 10.57)	6 (0.03, 11.96)
Montane grasslands and shrublands	11.26 (10.26, 12.27)	11.35 (10.39, 12.32)
Tropical and subtropical moist broadleaf forests	9.77 (5.34, 14.21)	21.49 (10.53, 32.44)

Table 1. Projected changes (% change) in the extent India's major ecological biomes by 2070 under RCP 4.5 and RCP 8.5 climate scenarios. Source: Rasquinha and Sankaran (2016). Values in parentheses are the lower and upper limits of the 95% confidence interval.

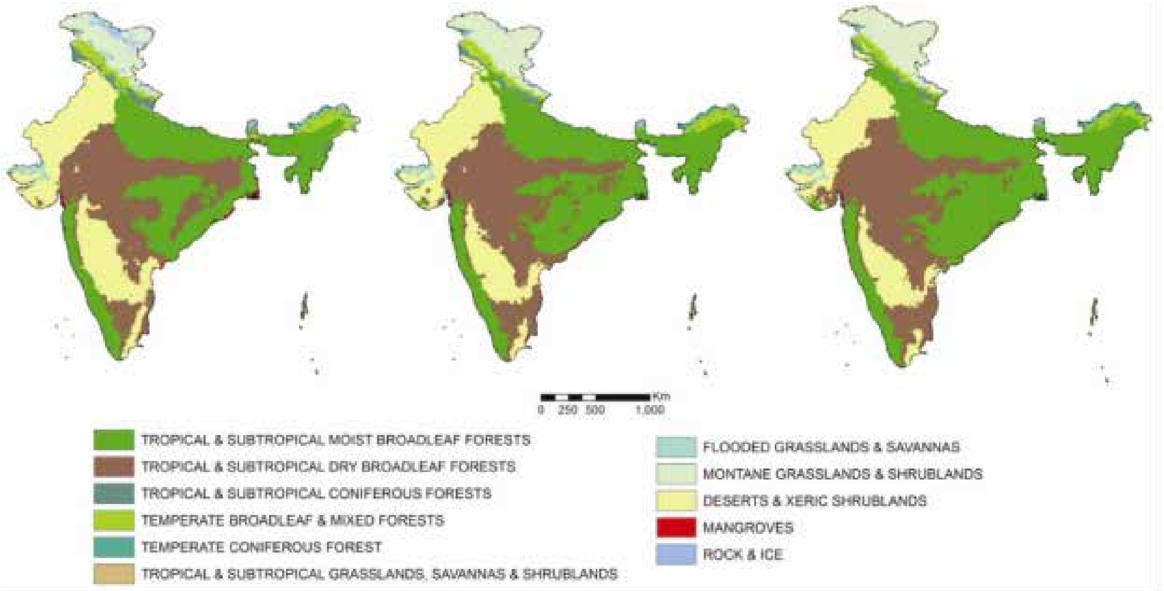


Figure 1. Current extent and distribution of India's major biomes and predicted extent and distribution of these biomes in 2070 under RCP 4.5 and RCP 8.5 climate scenarios. Source: Rasquinha and Sankaran (2016). Reproduced with permission from Current Science. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

Ecosystem Services: Definitions and Classification

In general terms, ecosystem services refer to the benefits that humans derive from the natural world (Daily 1997). These services and benefits are a product of the complex interplay between and amongst the ecosystem's physical or abiotic properties, such as temperature, moisture and nutrients, and biotic properties, such as the diversity and composition of its biological communities. The range and complexity of ecosystem processes and services that affect our day-to-day lives are invariably underappreciated – consider the water supply, crop pollination by bees, pest control by birds, microbial mobilisation of soil nutrients and primary production ecosystem services, to name just a few, that are essential for making a cup of coffee. A landmark paper by Costanza et al. (1997) estimates the annual global worth of ecosystem services as in the range of US $16-54 trillion, much of which remains unrecognised in conventional economic frameworks.

The broad classification of ecosystem services as provisioning, regulating, cultural and supporting types of services by the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005) has gained wide acceptance. Provisioning services include material benefits such as food and timber, regulating services modulate atmospheric composition and air and water quality, and cultural services represent aesthetic, spiritual or recreational values that humans derive from nature – these different services arise from fundamental supporting services such as nutrient cycling and primary production through photosynthesis (Millennium Ecosystem Assessment 2005). However, there as yet does not exist an exhaustive list of ecosystem services, in part because different end users may prioritise different kinds of services, and because many ecosystem service values are subjective and difficult

	Ecosystem service	Description or example
1	Gas regulation	Balance of CO_2 and O_2 in the atmosphere
2	Climate regulation	Regulation of atmospheric greenhouse gases
3	Disturbance regulation	Protection from storms
4	Water regulation*	Regulation of hydrological flows
5	Water supply*	Water in reservoirs
6	Erosion control and sediment retention	Prevention of soil loss due to wind or rain
7	Soil formation	Weathering of rocks
8	Nutrient cycling	Nitrogen fixation
9	Waste treatment	Breakdown of toxins and pollutants
10	Pollination	Pollination of agricultural crops by insects
11	Biological control	Biological pest control by birds
12	Refugia	Habitats for native species
13	Food production	Production of crops
14	Raw materials	Fuel and timber
15	Genetic resources	Medicinal plants
16	Recreation	Eco-tourism
17	Cultural	Spiritual values such as sacred groves

Table 2. List and brief descriptions of 17 ecosystem services described by Costanza et al. (1997).

**water supply and regulation are considered a single service in the review of Indian literature on climate change and ecosystem services.*

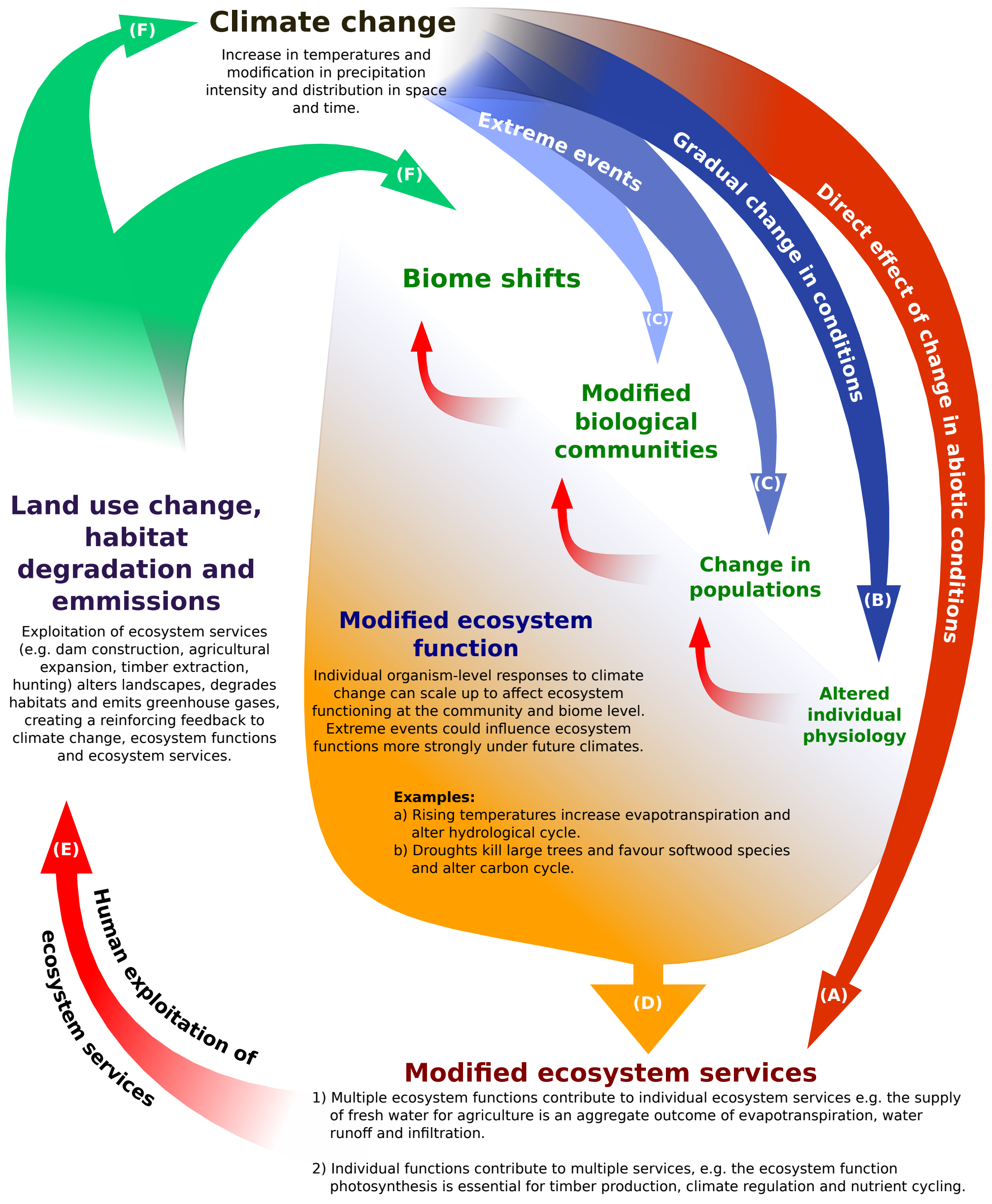
to quantify (Wallace 2007; Fisher and Kerry Turner 2008). Questions also prevail about the inclusion of ecosystem disservices, such as economic losses and threats to personal safety that are associated with living alongside large wildlife (Dunn 2010; Lele et al. 2013). A detailed assessment of the heterogeneity and uncertainty regarding the definitions and classifications of ecosystem services is beyond the scope of the present article. For consistency within this article and with other prominent literature on the field, we adopt the classification of 17 ecosystem services by Costanza et al. (1997) (Table 2).

To aid our understanding of the mechanisms by which climate change modifies biotic factors resulting in changes in ecosystem services, it is useful to view the biosphere's biotic constituents as a hierarchy of biological organization – scaling up from individuals to populations and communities of different species, and ultimately to the biome scale. It is also helpful to consider that ecosystems feature numerous interactions between individual organisms, within the same trophic level (e.g. competition) and across trophic levels (e.g. predation).

All levels of biological hierarchy, and interactions between different levels, contribute to the functioning of ecosystems and services derived from them. For example, growth rates of fuel-wood species (which are individual physiological responses to light, soil and nutrients) and their population sizes (which are partly the outcome of competition with other species) can impact fuel availability and livelihoods (Konwer et al. 2001; Kataki and Konwer 2002; Upadhaya et al. 2017). At a higher level of organization, which species make up the community of soil microbes can strongly influence the soil ecosystem's ability to make nutrients available for plant growth. Additionally, these microbial communities, as well as forest tree stands, contribute to the absorption and storage of carbon. In agricultural landscapes, invertebrate communities can provide a balance between pollination and pest control services (Campbell et al. 2012; Perović et al. 2018), thereby aiding food production, as well as the growth and stability of local and regional economies. At the coarsest scale of biological organization in this framework, biomes provide a more overarching set of services, a consequence of the interactions between numerous biotic processes within them. The most well-known amongst biome scale services is that of carbon sequestration and climate regulation attributed to forest ecosystems (Pan et al. 2011). Other important examples include the stabilisation of water supply and quality by wetlands (Mitsch et al. 2015), and the provisioning of biomass needs of rural populations and their livestock provided by mixed tree-grass ecosystems - such as savannas (Scholes and Archer 1997). Ultimately, ecosystem function, i.e. an explicit biological and/or biogeochemical process, or a combination of ecosystem functions, is responsible for the delivery of every ecosystem service (which is a human-centric concept). Hence, ecosystem services are the benefits humans derive from the biosphere mediated via ecosystem functioning. For example, the ecosystem service of fuelwood provisioning by a tree is essentially the consequence of the tree's photosynthetic productivity – a physiological process of the tree governed by abiotic conditions, such as temperature and resource availability. Similarly, carbon sequestration by tropical forests is determined by how much biomass forests accumulate, which in turn is determined by the difference between the biomass produced by the forest stand through photosynthesis and how much of it is lost through respiration. In this latter example, even though the realised service is perceived to be derived at the scale of the biome, or even the community, the fundamental process that contributes to the service operates at the scale of an individual, i.e. the net productivity of individual trees. This concept of performance of individuals scaling up to populations, communities and biomes is key to understanding how climate change will impact ecosystem services.

Climate Change and the Pathways for the Modification of Ecosystem Services

The effects of climate change on ecosystem services accrue through changes in both abiotic and biotic components. Figure 2 is a simplified schematic representing the pathways by which climate change potentially influences the supply of ecosystem services, and the reinforcing feedback that humans, in exploiting ecosystem services, potentially impose on climate change. The abiotic pathway of climate effects on ecosystem services (link A in Figure 2) is perhaps the most straightforward and well understood – for example, an increase in rainfall would be expected to increase the total amount of water flowing in streams, irrespective of ecosystem type. Among biotic pathways, climate effects at the level of individual organisms might have the most pervasive impact on ecosystem services (link B), especially if we consider the more 'gradual' component of climate change. Modifications



Increase in temperatures and modification in precipitation intensity and distribution in space and time.

Exploitation of ecosystem services (e.g. dam construction, agricultural expansion, timber extraction, hunting) alters landscapes, degrades habitats and emits greenhouse gases, creating a reinforcing feedback to climate change, ecosystem functions and ecosystem services.

Individual organism-level responses to climate change can scale up to affect ecosystem functioning at the community and biome level. Extreme events could influence ecosystem functions more strongly under future climates.

Examples:

a) Rising temperatures increase evapotranspiration and alter hydrological cycle.
b) Droughts kill large trees and favour softwood species and alter carbon cycle.

1) Multiple ecosystem functions contribute to individual ecosystem services e.g. the supply of fresh water for agriculture is an aggregate outcome of evapotranspiration, water runoff and infiltration.

2) Individual functions contribute to multiple services, e.g. the ecosystem function photosynthesis is essential for timber production, climate regulation and nutrient cycling.

Figure 2. Schematic diagram showing some of the major pathways through which climate change can affect ecosystem services, and the reinforcing feedback of human impacts on climate change and ecosystem services.

at the higher levels of organization will likely be observed as effects on individuals scale up, but there is also the potential for climate change to have direct effects at the population and community scale, as might occur during extreme weather phenomena, such as droughts or heavy rainfall events (link C). Such events would likely be indiscriminate in their impacts across species in a community, and could play a greater role in shaping ecosystem responses to climate change if extreme events increase in intensity and frequency, as is predicted by climate models (IPCC 2018).

Human exploitation of ecosystem services, including the unsustainable extraction of lucrative services, can alter land cover, degrade ecosystems and increase emissions (link E). These processes could result in reinforcing feedbacks, and thereby close the loop back to the original drivers of climate change and change in ecosystem functioning (link F). Chief among these are human impacts on the carbon cycle, which is modified along two key pathways. First, emissions from human activities, particularly from fossil fuel combustion (Pan et al. 2011), release carbon from terrestrial pools to the atmosphere as CO_2 – a potent greenhouse gas. Secondly, land clearing activities – such as those for development and agricultural expansion – reduce the cover of vegetation types, such as forests, diminishing the biosphere's ability to absorb and store this newly released carbon (Baccini et al. 2017). Hence, the carbon cycle is increasingly being 'skewed', with the accumulation of carbon in the atmosphere as CO_2. The resultant increases in atmospheric temperatures can have a knock-on effect on the hydrological cycle, which determines the distribution of precipitation over the Earth in both space and time. This linkage between human activities, the carbon cycle and the hydrological cycle forms the broad basis for predicted future conditions in a changing climate, i.e. an increase in global temperatures coupled with increased variability in the spatio-temporal distribution and intensity of precipitation (IPCC 2014). It is important to note here that human activities also significantly modify other biogeochemical cycles, such as those for nitrogen and phosphorus (Vitousek et al. 1997; Bennett et al. 2001; Phoenix et al. 2006; Galloway et al. 2008) – key elements for the biosphere's biotic components. Links between alterations in the cycling of these nutrients, carbon and water have the potential to exacerbate (Phillips et al. 2009; Doughty et al. 2015) or to some degree even mitigate (Melillo et al. 2011) the effects of climate change, and in turn, impact the delivery of ecosystem services. However, quantifying these links have thus far received limited research emphasis.

LITERATURE REVIEW: CLIMATE CHANGE AND ECOSYSTEM SERVICES RESEARCH IN INDIA

In this section, we review the state of current knowledge on the effects of climate change on ecosystem services in India. A systematic search of the scientific literature was conducted using the Google Scholar platform (https://scholar.google.com/), which was selected because of its relatively wider coverage of international and national publications compared to other academic search engines. We searched the titles and abstracts of literature published during the 2000-2018 period for the phrases "climate change" and "India". We then manually examined the >1200 studies that met the search criteria and retained studies focusing on ecosystem services, as defined by Costanza et al. (1997). For each study thus identified, we extracted information on (1) type of study – empirical (observational or experimental), modelling or review; (2) year of publication; (3) ecosystem service as defined by the study; and (4) closest matching ecosystem service category in Costanza et al. (1997). Further, we summarised the salient findings of the research on ecosystem services in India and identified key gaps, particularly with regard to ecosystem services derived from natural ecosystems.

Our literature review identified 102 studies published between the year 2000 and the present on the topic of climate change impacts on ecosystem services in India (Appendix A). The frequency of research on climate change and ecosystem services increased from around one study per year during 2000-2005 to over 13 studies per year since 2015 (Figure 3).

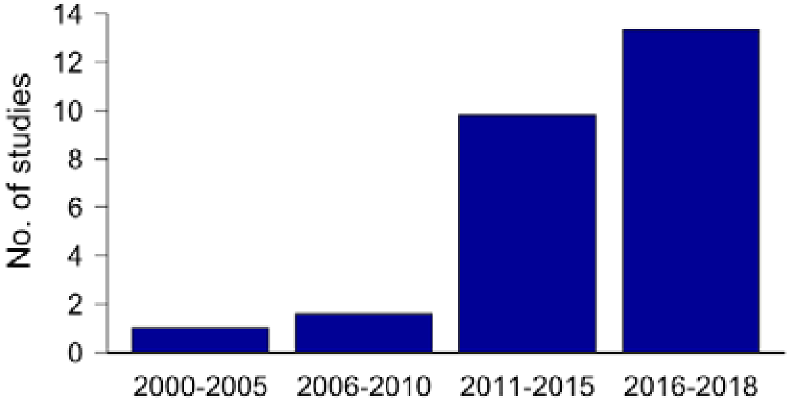


Figure 3. The average number of studies on climate change and ecosystem services in India per year across different time period during 2000-2018

Around half of all studies addressed the responses of crop production to climate change (Costanza et al. (1997) category "Food production") and a further 30% of the studies addressed aspects of water supply and regulation (Figure 4). The remaining 20% of the studies covered eight other ecosystem service types as defined by Costanza et al. (1997) (Figure 4), while seven ecosystem services, namely gas regulation, soil formation, nutrient cycling, raw materials, recreation and cultural, were not recorded in the reviewed literature. The large majority of studies (68%) employed modelling approaches to examine potential responses of ecosystem services to future climate scenarios, while empirical studies based on observations of ecosystem service responses to variation in climate over the last few decades, or experimental manipulations, comprised 16%, and reviews comprised 13% of all studies.

The body of research suggests that climate change is likely to negatively impact food production in India on the whole, but that the responses of crop yields might vary considerably by crop type and region. Increasing temperatures have been experimentally shown to reduce growth and development of cereals such as rice (Geethalakshmi et al. 2017), and increased drought and extreme rainfall over the latter half of the 20th century have been linked to reductions in rice yields.

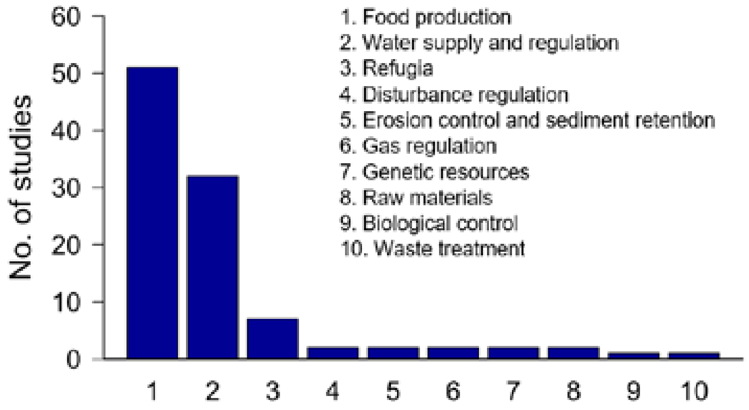


Figure 4. The number of scientific studies on the effects of climate change on different ecosystem services in India published during 2000-2018

Using crop simulation models (e.g. InfoCrop) to model crop yields under different climate scenarios, studies predict reduced yields of cereal crops such as rice, wheat and maize in many parts of the country, although some cooler regions could witness temperature-mediated increases in productivity (Byjesh et al. 2010; Soora et al. 2013).

The negative effects of temperature on crop yields could be mitigated by increases in precipitation in some regions and by improvements in productivity under elevated CO_2 concentrations, although the nature and magnitude of such CO_2 fertilization effects remain a matter of debate (Saxena and Kumar 2014; Abeysingha et al. 2016). While some crops might decline under a warmer climate, others could become more productive (e.g. coconut: (Kumar and Aggarwal 2013)), suggesting that climate change could necessitate shifts in the extent and distribution of different crops, as well as the development of climate-resistant varieties (Dutta 2014). Climate change is also likely to have substantial impacts on fisheries, with increasing temperatures being associated with reductions in spawning, altered distribution and ecology of commercially important fish species in inland and coastal ecosystems (Vass et al. 2009; Das et al. 2013; Zacharia et al. 2016).

Changes in climate are expected to alter the supply and regulation of water in India in a variety of ways. Glaciers are shrinking due to elevated temperature in the Himalaya mountains (Kumar et al. 2007; Mehta et al. 2014) – widely regarded as the 'water towers' of Asia – and this is predicted to substantially reduce water availability in densely populated downstream areas, especially in the Indus and Brahmaputra basins over the next 30 years (Immerzeel et al. 2010). In rain-fed river basins, rising temperatures are expected to increase evaporation and evapotranspiration (Priya et al. 2014) and drive widespread reductions in stream flow (Gupta et al. 2011), while stream flow and groundwater recharge in some regions could increase due to increases in precipitation (Gosain et al. 2011). In regions that

In addition to climate change, resource and land use by humans is likely to strongly affect future delivery of ecosystem services in India (Photo: P Jeganathan; Wikimedia Commons) are likely to witness increased rainfall and/or increases in extreme rainfall events, the ability of hydrological systems to regulate disturbances such as floods might also be reduced (Guhathakurta et al. 2011).

In India's heavily human-modified landscapes, the effects of climate change on hydrological functions could be exacerbated by land use and land cover change (Madhusoodhanan et al. 2016). For example, disturbances such as forest degradation and excessive livestock grazing, which are prevalent across the country, reduce the ability of hydrological systems to buffer against extreme events such as floods and droughts (Mehta et al. 2008; Krishnaswamy et al. 2012).

In addition to altering the quantity of water resources, climate change can also affect water quality; for example, increased temperatures are predicted to reduce the concentration of dissolved oxygen in stream water (Rehana and Mujumdar 2011), while greater streamflow under an increased precipitation regime could reduce concentrations of nutrients such as nitrogen and phosphorous (Jin et al. 2018). Further, increasing salinity of major rivers in North and Central India and saline intrusions upstream of river estuaries and deltas are expected to have profound impacts on both water resources and food production in these densely populated areas (IPCC 2018).

The alteration of stream flow due to climate change can in turn affect the ability of hydrological systems to control erosion. Modelling studies from hilly areas of Uttarakhand and central India predict that increases in stream flow due to precipitation and extreme events can reduce sediment retention in river systems, with the extent of soil erosion losses also influenced by soil type, topography and land use change (Mondal et al. 2016; Khare et al. 2017).

Changes in climate can also alter the potential for habitats to serve as refugia for biodiversity. Studies suggest that changes in temperature and precipitation could alter the distribution of India's major biomes during this century (Ravindranath et al. 2006; Rasquinha and Sankaran 2016), which could have implications for numerous native species associated with specific biomes. Recent work from India has focused on the climate threat to vulnerable ecosystems such as mangroves (Srivastava et al. 2015; Khan et al. 2016) and coral reefs (Raj et al. 2018), and vulnerable high-altitude species such as the Nilgiri tahr (Sony et al. 2018).

CONCLUSIONS

Our literature survey highlighted that the effects of climate change on ecosystem services is a topic of considerable scientific interest in India, with a rapidly growing number of studies from an impressive breadth of institutions across the country. Research so far has focused primarily on trying to understand and predict how two kinds of services – food production, and water supply and regulation – might be affected under a changing climate. Studies on food production chiefly correspond to climate-induced changes in crop physiology (link B of Figure 2), while studies on water supply and regulation mainly address abiotic processes (link A of Figure 2). At the same time, ecosystem services such as nutrient cycling and carbon storage, which emerge out of more complex ecological interactions between organisms and across levels of biological organization (links B in Figure 2), remain understudied in the Indian context.

Research is needed to better understand the impacts of climate change on culturally and economically important non-timber forest products in India (Photo: Venkat Ramanujan)

The research arena in India is dominated by studies that employ modelling approaches, which are undoubtedly essential for predicting the impacts of climate change on ecosystem services, but more emphasis is needed on simultaneously developing empirical lines of research. Studies on the responses of ecosystem functions and services to experimentally altered temperature, moisture and ambient CO_2 levels (e.g. Geethalakshmi et al. (2017)), and long-term ecological monitoring of ecosystem functions and services in relation to intra- and inter-annual variation in climate (e.g. https://lemonindia.weebly.com/), will serve to complement and enrich modelling-based assessments. Improved predictions of the nature and geographic variation of climate change in India, built from higher resolution climate models that capture the spatial heterogeneity and the fine-scale processes that shape precipitation changes, are also important for improving the scope of modelling-based assessments of ecosystem services. Further, higher-resolution historical climate data from local meteorological services can enhance our understanding of the relationships between local climate and ecosystem services.

While there is a general need to expand the suite of ecosystem services being studied, a few stand out as being especially important but understudied ecosystem services in the Indian context. First, there is need to better understand the impacts of climate change on the supply of non-timber forest products (NTFPs) such as honey and *Tendu* leaves, and genetic resources such as medicinal plants, which are economically vital for many rural and forest-dwelling communities across India. While there is anecdotal evidence that changes in flowering and fruiting patterns (due to altered climate) could pose a threat to the availability of a number of NTFPs (Basu 2010; Negi et al. 2012), there is clearly a need for a better conceptual understanding and quantification of the response of NTFP systems to climate change. Similarly, more research is needed into the role of ecosystems in buffering outbreaks of vector-borne diseases such as malaria, and into the possibility that the

Photo: Shreekant Deodhar

threat of such diseases could be exacerbated with increased temperatures and more variable precipitation regimes (Bhattacharya et al. 2006; Dhiman et al. 2010).

Second, there is need for research examining the impacts of climate change on carbon and nutrient cycling, because these are crucial ecosystem services from the point of view of mitigating future climate change, and because such research would support India's commitments towards international climate agreements (Government of India 2015). While some modelling studies predict that increasing temperature and precipitation can enhance terrestrial net primary production in India's forests (Ravindranath et al. 2006), the effects of drought, which are known to reduce the carbon sequestration potential of forests in the Amazon (Phillips et al. 2009), are unknown in India. Research is also needed on the impacts of changing temperature and precipitation regimes on the activity and metabolism of soil microbes, which too can have implications for terrestrial carbon and nutrient cycling (Zhu and Cheng 2011).

Finally, in India's predominantly and increasingly human-dominated environment, it is important to recognise that climate change is but one of several stressors that will shape the supply of ecosystem services in the future. There is therefore need for research that integrates the responses of ecosystem services to climate change with responses to other major global change drivers such as ecosystem fragmentation, degradation and nutrient deposition. In theory, there is potential for these drivers to have synergistic effects that exacerbate threats to ecosystem services – for example, carbon storage losses due to drought might be amplified in forests that are fragmented because both drought and fragmentation are known to kill large trees (Laurance et al. 2000; Nepstad et al. 2007).

In another example, the deposition of nitrogen and phosphorous from agricultural and industrial sources can alter the growth and survival of tree seedlings, and thereby modulate dry forest ecosystem responses to fire and drought (Varma et al. 2017). Land use and habitat fragmentation can also modulate climate impacts on ecological fluxes, such as the movement of water through catchments (Gosain et al. 2011; Madhusoodhanan et al. 2016) or the dispersion of infectious diseases (Rulli et al. 2017). It is therefore essential to strengthen the scientific links between climate-focused research and research on other anthropogenic global change drivers, as a step towards developing effective strategies for mitigating and adapting to future trajectories of ecosystem services in India.

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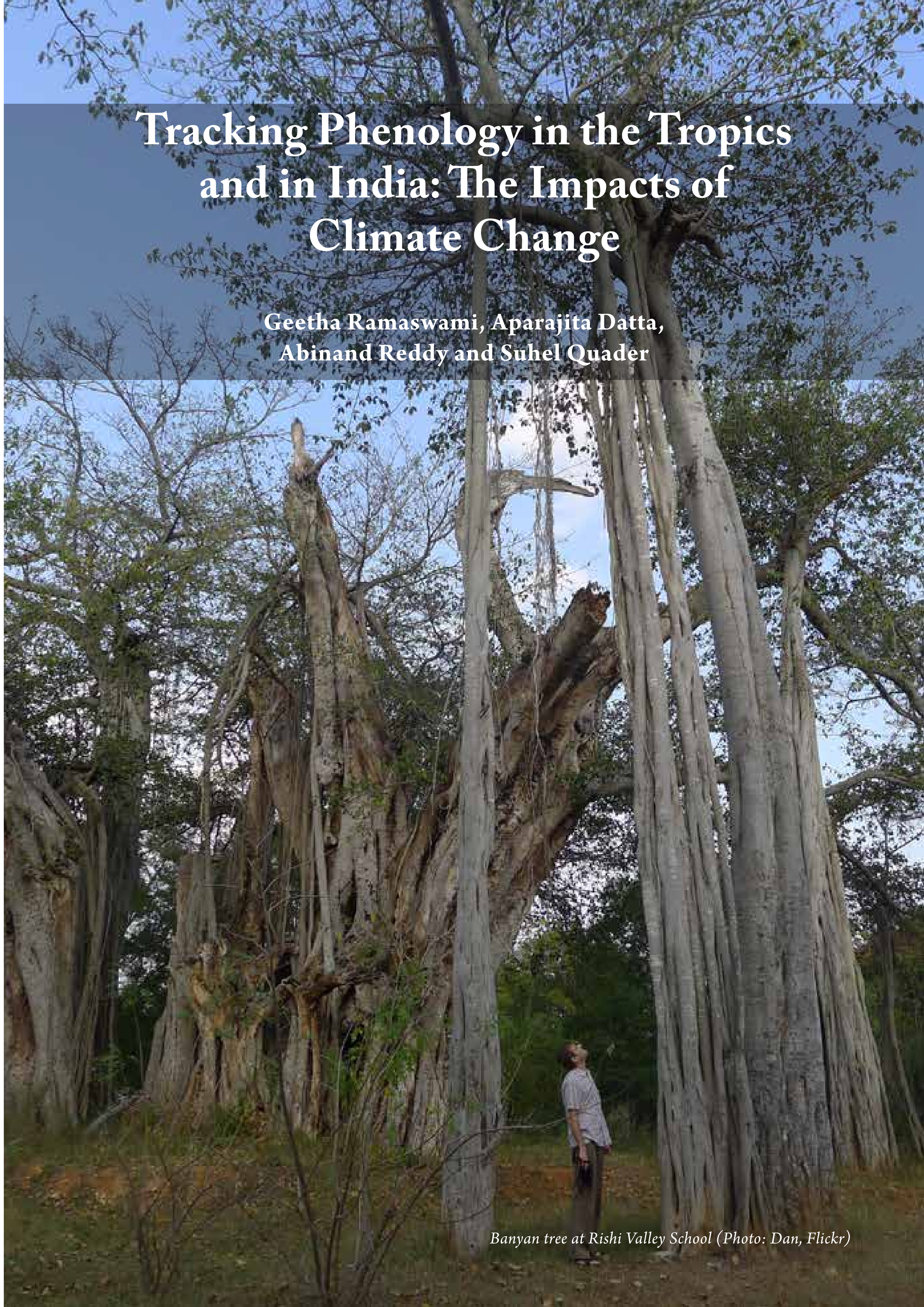
Tracking Phenology in the Tropics and in India: The Impacts of Climate Change

Geetha Ramaswami, Aparajita Datta, Abinand Reddy and Suhel Quader



Banyan tree at Rishi Valley School (Photo: Dan, Flickr)

INTRODUCTION

Phenology is the study of cyclical, predictable changes that occur in the life cycles of plants and animals. Such cyclical changes are ubiquitous in nature. Mature terrestrial angiosperm plants typically go through evident vegetative phenological phases such as leaf flush, leaf change or deciduousness, and reproductive phenological phases such as flowering and fruiting. The phenological cycles of plants have profound effects on the structure, composition and seasonality of animals, all of which depend on primary producers. This makes it important to understand the causes and consequences of phenological changes in our rapidly changing world.

The following review gives an overview of how terrestrial plant phenology is affected by various factors, with an emphasis on the role of climate change. This review is by no means exhaustive, but rather aims to provide a summary of the understanding of plant phenology from the tropics in general, and the Indian subcontinent in particular. The information reviewed here comes from a wide variety of methods - including historical and anecdotal records, direct observations and indirect observations via methods such as remote sensing.

DRIVERS OF PLANT PHENOLOGY

In evolutionary terms, plants are expected to be under selection to match their phenology with appropriate conditions. For example, in tropical forests that experience seasonal water stress, dry-season deciduousness is a prevalent phenological plant trait, and leaf fall coincides with peak dry season (Ouedraogo et al. 2016; de Camargo et al. 2018). Similarly, reproductive phenology of plants may be timed to match the availability and phenology of mutualists such as pollinators and seed dispersers. At a population or community level, plants may be adapted to synchronize reproductive phenophases (such as flowering) in order to ensure high pollination success or seed set (e.g. Bolmgren and Eriksson 2015; Rodríguez-Pérez and Traveset 2016). Further, fruiting peaks may be possibly correlated with local and long-distance seasonal migration of frugivores, as well as with the abundance of resident frugivores (e.g. Kimura et al. 2001; Burns 2002). When seeking to investigate the role of biotic factors such as pollinators or dispersers in driving flowering or fruit ripening times, there is a problem of circularity, with cause and consequence being indiscernible.

Plant phenology may be influenced by a number of biotic and abiotic drivers that can influence the onset and duration of phenophases. Vegetative and reproductive phenology of plants may be affected by biotic stressors such as herbivores and pathogens. Herbivory by insect pests induces delayed vegetative growth and flowering in plants (e.g. Lehndal and Ågren 2015; Lemoine et al. 2017). The converse - plant phenology affecting the phenology and abundance of herbivores - is also reported (e.g. Posledovich et al. 2015; Velasque and Del-Claro 2016). Furthermore, biotic factors seldom act independently of the prevalent abiotic factors, and the effects of the former are often confounded by the latter (e.g. Rodríguez-Pérez and Traveset 2016; Tunes et al. 2017).

Abiotic factors such as growth-season temperature, duration and intensity of precipitation, water stress, and duration of solar irradiance have been shown to affect the vegetative and reproductive phenology of plants across latitudes and in a variety of habitats. Leaf production and growth have been shown to be positively correlated with seasonal rainfall (February and Higgins 2016; de Camargo et al. 2018). The phenology of flower and fruit production of tropical trees is influenced by several environmental factors such as temperature, light, rainfall, relative humidity, solar radiation, as well as edaphic factors (Janzen 1967; Frankie et al. 1974; Opler et al. 1976; Foster 1982; Borchert 1983; Rathcke and Lacey 1985; Ashton et al. 1988; Kinnaird 1992; van Schaik et al. 1993; Tutin and Fernandez 1993; Chapman et al. 1999). The major abiotic factors that have been identified as cues for flowering are photoperiod, temperature, and moisture (see Rathcke and Lacey 1985; Chapman et al. 1999). Recent long-term phenological studies in some tropical ecosystems have revealed that flowering onset and duration, and fruiting frequency and intensity are induced by duration and intensity of solar irradiance (Babweteera et al. 2018; Chapman et al. 2018; Wright and Calderón 2018). Studies from Neotropical, African, and South East Asian forests have noted that the peak of animal-dispersed fleshy fruits occurs in the rainy season (Foster 1982; White 1994; Kitamura et al. 2002) or at the end of the rainy season (Chapman et al. 1999). Intensity of fruiting has also been shown to be positively affected by higher rainfall, and peak fruiting in tropical species often coincides with the peak of the rainy season (Dunham et al. 2018; Mendoza et al. 2018).


Flowers of Horsfieldia kingii *(Myristicaceae) which is a species of wild nutmeg found in north-east India (Photo: Aparajita Datta)*

Global warming induced climate change is likely to affect all of the above-mentioned abiotic factors. The following sections address how tree phenology is likely to change with changing climate, and what the consequences are of altered phenology on downstream trophic interactions.

EFFECTS OF CLIMATE CHANGE ON PHENOLOGY

Most of the understanding about the effects of climate change on plant phenology comes from temperate regions, where phenomena such as leaf budburst or synchronous flowering are known to be affected by average springtime temperature or photoperiod or a combination of the two (Fitter et al. 1995; Basler and Körner 2012, 2014; Way and Montgomery 2015; Wang et al. 2018). Alterations in the onset of a season or average seasonal temperature may advance or delay the onset of a phenophase, with consequences for downstream trophic, population and community processes (see next section). Changing phenology may also feed back into climate phenomena such as albedo seasonality and CO_2 flux, which may further affect climate change at local or regional scales (Richardson et al. 2013). A number of studies from across the world have contributed to the understanding of plant phenological responses to seasonality and climate change (Figure 1). Below we summarise evidence for climate-change induced alterations in tree phenology, separately for temperate and tropical regions of the globe.

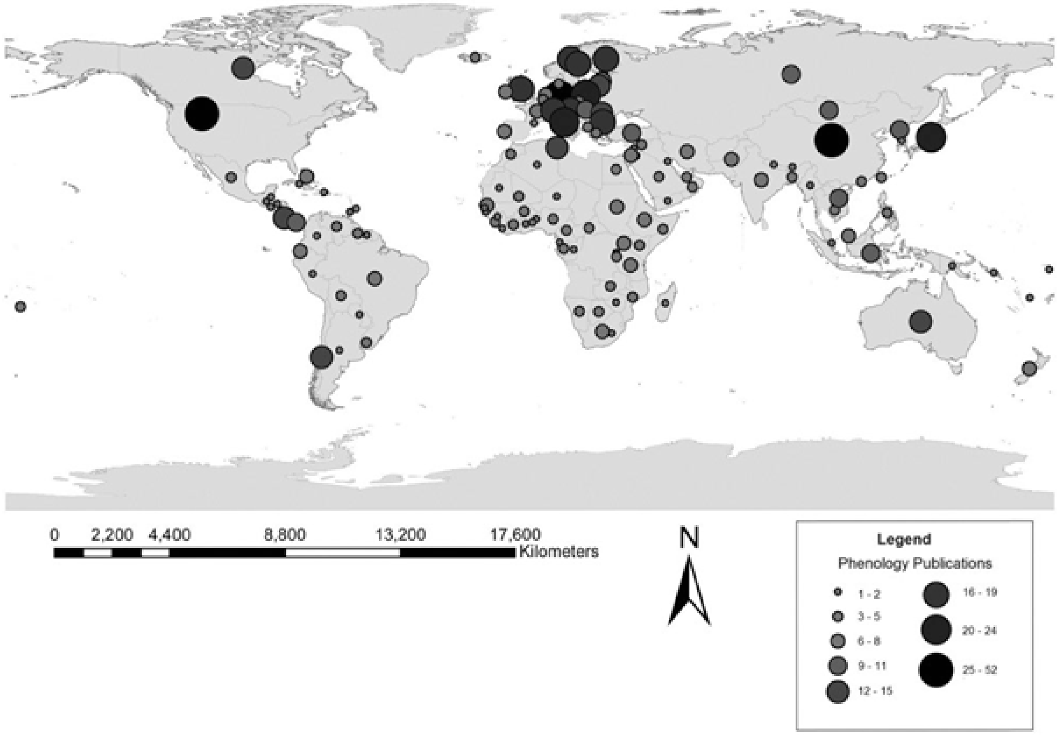


Figure 1. Global distribution of phenological studies based on publication output (reprinted from Fitchett et al., Progress in Physical Geography (39):4, pp. 460-482, copyright © 2015 by ATREE. Reprinted by Permission of SAGE Publications, Ltd.). Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries

Phenology and Climate Change in Temperate Regions

One of the best-known examples of phenology influenced by climate change comes from long-term records of flowering in *Prunus jamasakura* (Japanese cherry) in Kyoto. Data collected over the span of eight centuries, collated from diaries and personal records, shows that date of full flowering in trees was inversely correlated with mean temperature in March (Aono and Kazui 2008). The long-term data showed high inter-annual variability in flowering dates, but no advancement in flowering dates until the early 1900s (Menzel and Dose 2005; Parmesan 2006), presumably due to increasing average temperatures in March. In England, trends in century-long data on vegetative phenology such as leaf emergence indicate an average advancement of 2.5 days per century for 13 species in the onset of leaf flush accompanying warming climate (Thompson and Clark 2008). In the northern latitudes (for example, 42-45 °N in the USA), with increasing temperatures, growing seasons for tree species may have also lengthened (White et al. 1999; Parmesan 2006 and references therein).

Responses of phenological events to changing climate may be affected by the timescale at which these events are analysed. For instance, in a 57 year (1959-2016) assessment of the community-level phenology of urban tree species in the Pacific Northwest of the USA, spring phenophase onset was advanced for 80% of the species examined, likely driven by increasing spring temperatures. However, a shorter time period of 21 most recent years (1996-2016) showed no signal of climate-change driven alteration of phenophase onset; instead, phenology was correlated with a recurrent weather phenomenon - the Pacific Decadal Oscillation (Lindh et al. 2018). Thus, long-term phenological responses may reflect actual climate change, while shorter-term trends might indicate variation due to local weather phenomena.

Phenology and Climate Change in the Tropics

In most of the tropics, seasonal variability in temperature may not be as pronounced as seasonal or inter-annual variability in precipitation (Corlett and Lafrankie, Jr. 1998). In contrast to temperate regions, the drivers of plant phenology in the tropics are poorly understood (Richardson et al. 2013), and the response of plant phenology to climate change even less so. In the tropics, variability in phenological responses to seasonal abiotic factors is not well known, and phenological response to seasonal variation in temperature and precipitation is very diverse (Corlett and Lafrankie, Jr. 1998).

Few case studies have explored the effect of climate change on phenological responses over different spatial and temporal scales. At the landscape level, a recent study from Ethiopia used data for 14 years (2002-15) derived from remote sensing images, and found a trend similar to that in temperate regions: the overall growing season of vegetation had become longer and the growing season onset had also advanced. This change in phenology was highly correlated with increasing variability in the onset of the high-rainfall season. Furthermore, in contrast to temperate regions, vegetation greening was found to be inversely correlated with increasing temperature across the country (Workie and Debella 2018). At the regional level, a study from Xishuangbanna, China, reported that of 21 species examined over a period of 27 years, 7 species showed a delay in budburst, 4 species showed an increase in the growing season, and 5 species showed a shortened flowering period. Vegetative phenology trends were found to be correlated with increasing temperature while flowering phenology change was found to be correlated with decreased solar irradiance duration in the rainy season (Zhao et al. 2013).

Plant phenology in the tropics is also known to respond to global-scale weather phenomena like the El Niño Southern Oscillation (ENSO). ENSO is a large-scale, irregular event characterised by the warming of the sea surface in the eastern tropical Pacific Ocean, which affects the climate of much of the tropics. ENSO typically occurs every 2-7 years, and may cause sea surface temperatures to rise by 0.5 (low-intensity ENSO) to > 3°C (high-intensity ENSO) (Capotondi et al. 2015). Plant phenology and phenological strategies have been shown to respond to ENSO-driven weather events. For example, in Kibale National Park, Uganda, fruit production in trees was positively correlated with average monthly solar irradiance and the occurrence of ENSO (measured as a composite index of sea-surface pressure and temperature, surface wind and cloudiness) in the previous 24 months (Chapman et al. 2018). In Panama, leaf-fall generally precedes seasonal maximal solar irradiance and water deficit, while seed-fall from abiotically dispersed plants lags behind peak seasonal water deficit (Detto et al. 2018). However, during ENSO, seed-fall phenology was found to be concurrent with peak water-deficit. Thus, ENSO was associated with a shift from predominantly vegetative leaf phenology to that of a predominantly reproductive fruiting phenology, presumably to cope with high light and low water availability (Detto et al. 2018).

Extreme ENSO events result in extreme local weather such as floods and droughts in the tropical regions affected by these oscillations, and plant phenology may respond accordingly. For instance, irregular phenology - such as the retention of leaves on water-stressed deciduous trees, and leaf-flushing in mid-dry season following an abnormal rain event - was reported following an ENSO-driven drought in a semi-deciduous forest in Costa Rica (Borchert et al. 2002). ENSO events may also affect ecosystem properties like net primary productivity via changes in plant growth phenology. The length of the growing season for vegetation has been found to be negatively correlated with seasonal drought in some ENSO-affected areas such as the sub-tropical island of Taiwan (Chang et al. 2013). If ENSO-driven droughts were to increase in frequency and intensity, growing seasons of vegetation may get affected, eventually reflecting in reduced net primary productivity of the ecosystem (Chang et al. 2013). Attempts are underway to tease apart the natural variability in ENSO events from those that may be potentially driven by climate change. Given the poor predictability of whether ENSO events will occur more frequently or be more extreme, the consequences for tropical plant phenology are likely to remain speculative (Collins et al. 2010; Chen et al. 2017).

Consequences of Altered Phenology on Trophic Interactions

There are growing concerns about how phenological shifts due to climate change in primary producers might have cascading effects on higher trophic levels. A perspective that cuts across trophic levels may be vital to understand the real scale of disruptions by climate change and prioritise mitigation measures.

The timing of vegetative phenophases is directly critical for many herbivores. For example, the coupling of the phenology of winter moths and that of pedunculate oaks is a well-documented system in Europe (Buse et al. 1999; Visser and Holleman 2001). The moths appear to follow the evolutionary strategy of maximising reproductive output by synchronising larval emergence with leaf budburst in oaks. Further coupling is found down the trophic cascade: egg hatching of great tits is timed to match the larval emergence of winter moths to maximize food availability for the chicks (Cresswell and McCleery 2003; Visser and Both 2005). Reproductive phenology of other birds is also shown to match seasonal food availability in multiple systems (Baines et al. 1996; Pearce-Higgins et al. 2005).

Plant marking for phenology work (Photo: Aditya Harikrishnan)

Since reproductive phases of plants are similarly critical for their pollinating and fruit dispersing mutualists, decoupling of their phenophases can be detrimental to both sets of interactants. Multiple studies have investigated the phenologies of bees and the associated species they pollinate. While this system is more robust to climate change, where both the plants and the bees have been observed to advance their phenologies to adapt to climate change, hints of de-synchronisation are being observed (Hegland et al. 2009; Bartomeus et al. 2011). Similar studies have shown phenological associations of ants with the reproductive phenology of plants whose seeds they disperse, where plants are advancing their flowering and fruiting periods as a response to climate change, but ant phenology is advancing to a lesser degree and as a consequence, ants are now beginning to disperse seeds of different species (Warren et al. 2011).

With rapid changes in climate, the leaf-herbivore, flower-pollinator and fruit-disperser interactions described above may experience decoupling of their evolutionarily synchronised phenophases. The decoupling can happen either due to species tracking different environmental cues or because of differential responses to a common cue. In temperate regions, the latter is more apparent, as most species track temperature, but the degree to which they respond to warming may be different. In the oak-moth-tit example discussed above, warming has led to earlier bud burst. Larval emergence has also advanced but lags behind the onset of budburst. Similarly, the earlier egg hatching in tits lags behind the larval emergence (Visser and Both 2005). Phenology dependence and potential mismatch have also been shown in other species, such as in the golden plover, black grouse, puffins and European shag (Visser and Both 2005).

All the examples above come from temperate regions. In the tropics, species could track multiple climatic cues such as moisture, photoperiod and temperature, which makes ascertaining their individual and combined effects more complicated. Yet, studies have shown decrease in fitness of plant-eating animals due to the changing phenologies of their preferential dietary plants. For example, fruit scarcity was found to be associated with lower reproductive rate, or higher inter-birth interval in female chimpanzees of Kibale National Park, Uganda (Wrangham et al. 1998). While the tropics may be slightly buffered due to the inherent stochasticity of moisture availability and coevolved plasticity of phenophases, they face the risk of decoupling of phenophases by both mechanisms mentioned. In this light, further arguments have been made to unravel the effects of phenological mismatch in specialists versus generalist species dependent on plant phenophases and similarly in obligate versus facultative mutualists. It was initially assumed that specialists and obligate mutualists are likely to be more adversely affected, but theoretical arguments have been made that both may be equally at risk - as specialists and obligate mutualists are likely to track the same abiotic cue as their associated plant species while the generalists and facultative species may be tracking different cues (Rafferty et al. 2015).

THE CURRENT STATE OF PHENOLOGY RESEARCH IN INDIA

We carried out a literature review of phenological studies in India in terms of location, duration, questions examined, parameters measured and the main findings (Appendix B, Figure 2). Phenological studies in India have been largely restricted to dry deciduous forests and evergreen forests in south India (Prasad and Hegde 1986; Bhat 1992; Murali and Sukumar 1993; Ganesh and Davidar 1997, 2005) and fewer from tropical and sub-tropical moist forests in north-east India (Shukla and Ramakrishnan 1982; Barik et al. 1996; Kikim and Yadava 2001; Adhikari et al. 2015).

Possibly, the first ever formal phenological study in India was by Shukla and Ramakrishnan (1982) in Meghalaya, north-east India. Most subsequent studies have been from multiple sites in south India (Prasad and Hegde 1986; Bhat 1992; Murali and Sukumar 1993, 1994, Ganesh and Davidar 1997, 2005; Krishnan 2002; Sundarapandian et al. 2005; Selwyn and Parthasarathy 2006; Somasundaram and Vijayan 2010; Suresh and Sukumar 2011, 2018, Nanda et al. 2013, 2015), with a few from northern India in later years (Kushwaha and Singh 2005; Singh and Kushwaha 2005a, 2006, Bajpai et al. 2012, 2017; Chaurasia and Shukla 2016). There are a couple of published studies from eastern India (Mishra et al. 2006) and arid western India (Yadav and Yadav 2008).

Most phenology studies in India have been at the community level (large number of species selected based on abundance/dominance in the vegetation composition of the site), and the duration of most studies has been for 2 years (Appendix B), with only a few published studies being of longer duration (e.g. Datta and Rane 2013; Suresh and Sukumar 2018). The short duration remains a key limitation to an understanding of the causes and consequences of temporal changes in phenology.

Most studies describe the seasonal patterns of leaf flushing, flowering and fruiting with a few carrying out quantitative analyses relating these patterns to climate variables. Additionally, most earlier studies have used the number of species in leaf, flower or fruit as a measure for the timing and extent of the phenophases. However, currently, ongoing phenology monitoring studies use a proportion of trees in each phenophase as a measure of intensity, and additionally score phenophases on a scale from 0 to 4 (0 to 100% of the canopy) to characterize intensity of a phenophase within trees more quantitatively.

A few studies have qualitatively examined evolutionary questions related to biotic drivers of tree phenology such as insect herbivory for leaf flushing, pollinator guilds for flowering and dispersal guilds for fruiting (Murali and Sukumar 1993, 1994). All studies barring three (Nautiyal et al. 2001; Krishnan 2002; Joshi and Janarthanam 2004) have focused on trees alone. Joshi and Janarthanam (2004) examined the flowering phenology of endemic species in Goa which included monocots and dicots and varied life-forms (herbs, shrubs, trees, climbers), while Krishnan (2002) examined the reproductive phenology of 60 understorey species (herbs including orchids, shrubs and small trees) in a wet evergreen forest in the southern Western Ghats. We could only find a single study on the phenology of 171 species of grasses, herbs, forbs and shrubs in an alpine pasture at >3000 m elevation (Nautiyal et al. 2001) where they found that flowering occurred between May to August after snowmelt, with fruiting between June to August before senescence set in before the winter.

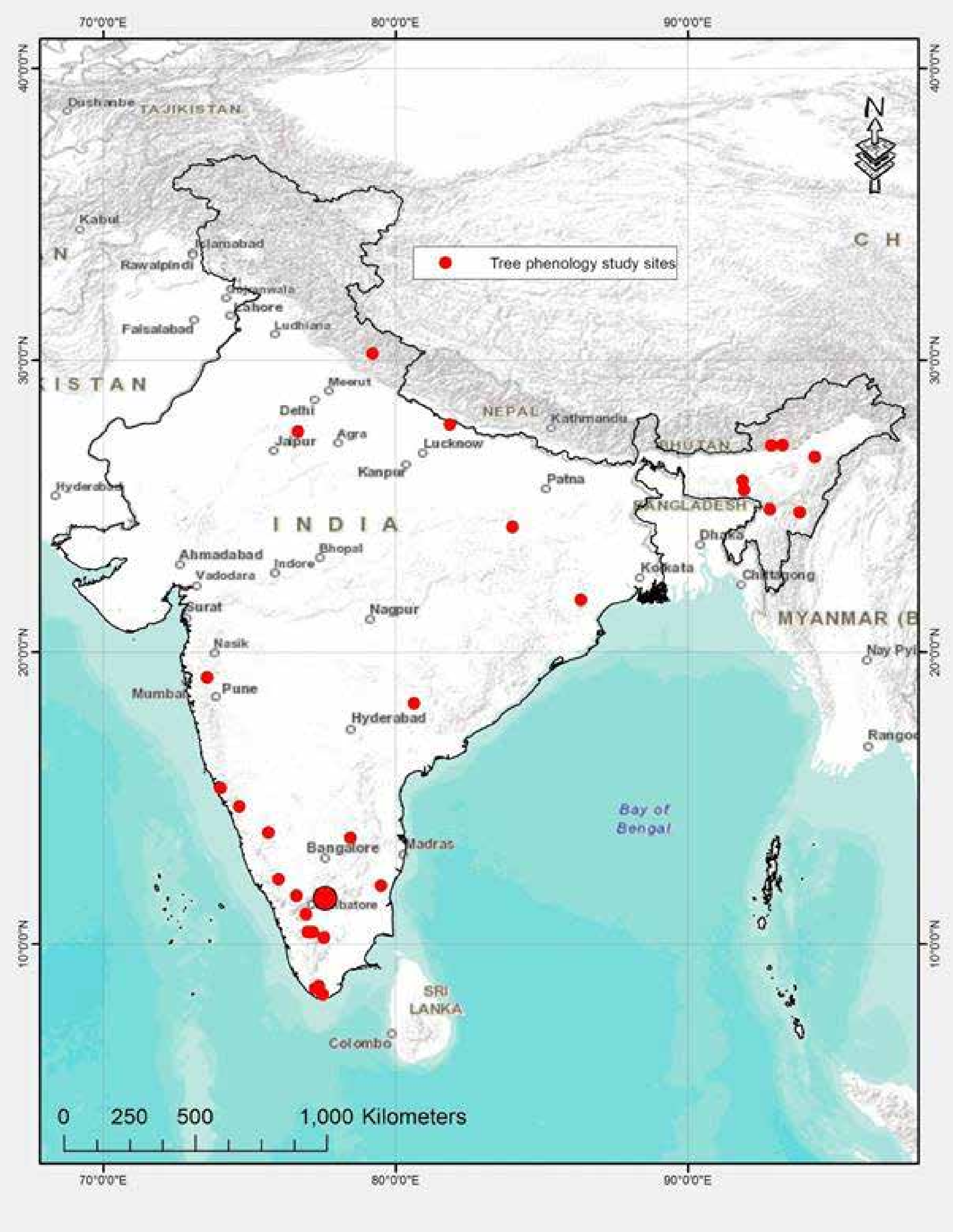


Figure 2. Locations of phenological studies from India (1982 - 2017) from Appendix B. Mudumalai Tiger Reserve in the state of Tamil Nadu (large red dot) is the site with the longest-running phenological study in India (Map prepared by R. Raghunath, NCF). Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

A few phenology studies have been on single tree species that are either rare or have an important functional role in the ecosystem (Ganesh and Davidar 1997; Datta and Rane 2013; Borah and Devi 2014; Chaurasia and Shukla 2016; Nath et al. 2016 - Appendix B). Below, we describe some of the key results for vegetative and reproductive phenophases from Indian studies.

Vegetative or Leaf Phenology

What is striking is that the timing of leaf fall and leaf flushing across India in varying latitudes and rainfall gradients appears to be very similar. In Uttar Pradesh at 24°N with 85-130 cm rainfall, leaf flush is from March-June, while leaf fall initiation and completion occurs between November and March (Singh and Kushwaha 2006), while a tropical semi-evergreen site in Odisha (21-22°) with higher rainfall also has leaf fall in March and leaf flush in April (Mishra et al. 2006). In drier Rajasthan (27-28°N, 70 cm), leaf fall occurs earlier in October-December, while the period of leaf flush is again in February-May (Yadav and Yadav 2008).

Shukla and Ramakrishnan (1982) and Kikim and Yadava (2001) also found that in Meghalaya (25-26°N, 220 cm) and Manipur (24°N), leaf flush occurred in the pre-monsoon period between March-June. Leaf fall was noted from January to March in Meghalaya, while it was post-monsoon in Manipur which was at a higher elevation and had mostly evergreen species. Studies from south India have mostly been in the Western Ghats, and the general patterns are similar with strong seasonality in leaf flush in the pre-monsoon dry period in February, with leaf abscission in December (Bhat 1992; Murali and Sukumar 1993; Sundarapandian et al. 2005; Nanda et al. 2015). However, at a higher elevation evergreen site, Nanda et al. (2015) found that leaf flushing occurred in January, while at the dry deciduous site, leaves flushed in April. In a low-elevation tropical semi-evergreen site (27°N) in Arunachal Pradesh, leaf flushing of most species (38-42 out of 54 spp.) occurred between April and August (Datta et al., unpublished data). It would be interesting to examine these patterns based on latitude/longitude/rainfall and elevation. It appears from these studies that elevation may play a role in differences in timing of leaf flush and fall.

The leafing phenology of deciduous species in dry tropical forest has been investigated by Kushwaha and Singh (2005), Singh and Kushwaha (2005a, b, 2006) and Kushwaha et al. (2011, 2015). Singh and Kushwaha (2005a) examined the paradox of *Shorea robusta*, a common tree species in dry and moist forests which has been described as deciduous, semi-deciduous and evergreen. They found through tagging twigs and doing monthly counts that leaf exchange is a survival strategy during the dry period, with old leaves being replaced by new leaves. They found that during the transition in leafing phenophases in March, there were phenological variants in leaf flush/leaf decay patterns in trees of *Shorea* indicating functional diversity. They conclude that *Shorea* is a semi-evergreen species, and its high adaptability allows for its wide distribution in the tropics. In another study at the same site, Kushwaha and Singh (2005) describe the patterns of leaf phenological diversity of nine tree species in a tropical dry forest – they show that trees showed a gradient of deciduousness ranging from semi-evergreen to species that were deciduous for 7 months. Based on their quantification of leaf flush/leaf fall initiation and completion, they identified 4 functional types that differed in degree and period of deciduousness. Conspecific trees showed asynchrony with respect to leaf flush completion and initiation and completion of leaf fall and extent of leafless period.

Ripe fruits of Horsfieldia kingii *(Myristicaceae). It is a dioecious species - only female trees bear fruit. Its large-seeded fruits are eaten and dispersed by hornbills and imperial pigeons (Photo: Aparajita Datta)*

Flowering and Fruiting Patterns

In general, flowering at most sites coincided with leaf flush or closely followed leaf flush in the early to late dry season, usually between February and May with a peak in March-April at many sites (Appendix B). In north Karnataka, there were two peaks in flowering in December and March (Bhat 1992), while further south on the east coast, flowering peaked in March (Selwyn and Parthasarathy 2006). In Odisha (Mishra et al. 2006) and Manipur (Kikim and Yadava 2001), flowering peaked in April-May and April respectively.

Murali and Sukumar (1994) found that overall flowering peaked in the dry season at one site and wet season in the drier site where soil moisture may have been limiting. They found that bird-pollinated flowers flowered in the dry season, which might have provided more visibility for large flowers in the leafless phase, while wind-pollinated species flowered in the wet season when pollen transport is facilitated by higher wind speeds. Insect-pollinated flowers showed no seasonality in one site, while showing flowering in the wet season in the drier site.

In Kalakkad Mundanthurai Tiger Reserve (KMTR), Tamil Nadu, Ganesh et al. (2017) have reported annual flowering in only 3 of the 70 species observed over a period of more than 20 years, and extremely sporadic mass flowering in species such as *Calophyllum austroindicum*. Ganesh et al. (2017) have anecdotally noted the importance of keystone species such as *Palaquium ellipticum* which attract seasonal insect pollinators such as *Apis dorsata*, and facilitate the pollination of other co-flowering tree species. In KMTR, pollination success in *Cullenia exarillata* over the long-term has been described (Ganesh et al. 2017). Here, reduced pollination success in disturbed or degraded areas has been attributed to fewer visits by mammalian pollinators, and to the increased loss of unpollinated flowers to infections due to unseasonal rain in the flowering season.

Fruit ripening and fruit fall peaked in the rainy season (Bhat 1992; Murali and Sukumar 1994; Sundarapandian et al. 2005). Murali and Sukumar (1994) found that fruiting peaked during late wet season extending into the early dry season, and time-lag correlation indicated that fruiting followed rainfall with a lag of about 2 months. In a tropical dry evergreen forest, fruiting peaked twice, in April (dry season) and September (wet season) (Selwyn and Parthasarathy 2006). In Odisha, fruiting peaked in May-June (Mishra et al. 2006). In higher elevation subtropical evergreen forest in Manipur, fruiting peaked in September-October (Kikim and Yadava 2001). Sundarapandian et al. (2005) suggested that these patterns are related to both abiotic and biotic factors and speculated that flowering coincides with leaf fall to attract pollinators, while fruiting in wet season occurs to utilize soil moisture for seed germination and seedling establishment. They also noted that several species did not flower during their 2-year study.

Ganesh and Davidar (2005) found that nine tree species fruited annually, seven fruited once in two years and the remaining species fruited once in several years. They found significant variation in fruit availability between years. Masting as a way of satiating high seed predation was limited to only a few tree species, though many suffered high seed predation. Supra-annual flowering/fruiting was also noted in a Myristicaceae species that is subjected to high seed predation, in two different study periods spanning 6 years in Arunachal Pradesh (Datta and Rane 2013).

A few studies have examined phenology from the perspective of seed predation and frugivores. Ganesh and Davidar (1997) examined the flowering phenology of *Cullenia exarillata*, a dominant evergreen species which flowers heavily and is consumed by arboreal vertebrates during fruit scarcity in the forest. They speculate that overabundance and timing of flowering could have evolved to satiate predators and enable pollination during a time of general fruit scarcity in the forest. They suggest that *Cullenia* is a keystone species in these forests. (Kannan and James 1999) found that fruiting of hornbill food plant species was seasonal from the dry hot season till early wet season which coincided with hornbill breeding from February to May. Fruiting was scarce from July to January (wet season). Fig fruiting was aseasonal and figs were available during general fruit scarcity playing a keystone role.

Patel (1997) suggested that the importance of figs as keystone resources is diminished if fig fruiting coincides with the fruiting period of non-fig species. She compared the leafing, flowering and fruiting of non-fig species with fig species at a deciduous and evergreen forest site. She found that individual fig trees produced crops one to three times annually, at different times of the year for different trees. While the fig community fruiting peaks in the evergreen site coincided with fruiting peaks of non-figs, in the deciduous site fig fruiting peaked slightly before non-fig fruiting peaks. The role of figs as key resources is likely to differ based on forest type, and depend on factors such as fig fruiting patterns, fig tree density and frugivore territoriality (Patel 1997). See Appendix B for more studies on fig phenology (Patel 1996; Suresh and Sukumar 2018).

Singh and Kushwaha (2005b) summarise key findings from phenological studies in tropical dry forests, and suggest that rainfall periodicity and soil water availability influence tree phenology, and that the wet season was associated with increase in growth while the dry season constrained growth. They identify that the future key research needs in the dry tropics are studying the extent of deciduousness, timing of vegetative bud break, leaf strategy, water relations, seasonal flowering types and asynchrony. They stress the need for long-term quantitative documentation of tree phenological patterns in India through a phenological station network in diverse climatic/vegetational zones. Recently, Kushwaha et al. (2011) have emphasized the need to develop predictive understanding of impending climatic change (i.e. precipitation and temperature) on phenophases diversity by collecting long-term data in the dry tropics.

There are a handful of sites in India (6) that have long-term data and most of these are currently ongoing, however none of these studies are published – these include Sukumar et al. data from Mudumalai, Tamil Nadu, which is ~30 years (although parts of this data are published and cited above), Ganesh et al. (2017) data from KMTR which is 20+ years, Datta et al. data from Pakke Tiger Reserve, Arunachal Pradesh, which is in two time periods, initially for 4 years (1997-2000) and later from 2009 and is ongoing, Quader, Reddy et al. data from a dry forest in Rishi Valley, Andhra Pradesh, which is ongoing for 10 years (see Appendix B). Some of the results from the latter two studies are highlighted in this chapter as case studies.

A long-term phenology study has commenced in Anamalai Hills in Tamil Nadu from 2017 (Srinivasan et al., unpublished data, Appendix B). Another project which has been ongoing for 6 years is examining the leafing, flowering and fruiting phenology of 79 woody species from a seasonally dry tropical forest in Nigdale, Maharashtra in the northern Western Ghats of peninsular India (Barua et al., unpublished data, see Appendix B). There is now data for 6 years for 24 species, and for 4 years for 79 species. Preliminary results for leaf phenology showed that quantitative indices of leafing behaviour represent a continuum as opposed to expectations from the discrete evergreen vs. deciduous categories. These quantitative indices were related to timing of leaf flush and senescence, indicative of light and water use strategies in these species. The results indicate that evergreen species flush leaves to coincide with the time of maximum light availability, while more deciduous species flush closer to the onset of the rains indicating greater water limitations. Congruent with this, Barua et al. (personal communication) found significant relationships between quantitative indices of leafing behaviour and leaf functional traits. Together, these results suggest that future predicted decreases in water availability may negatively affect more deciduous species than evergreen species in this region (Barua et al., unpublished data).

As is evident from the preceding section, studies need to span many years to understand seasonal and annual variations, climatic variability, and to detect changes in onset, timing, duration, quantum and synchrony in vegetative and reproductive phenology. Long-term studies in other regions like SE Asia, Neotropics, Africa and Europe/North America often span 10 to 30 years, and occasionally much longer. There is an urgent need for long-term phenology monitoring in India, and tools such as remote sensing and citizen science (Box 1) should be put to use in order to gather data. Below we present, two case studies from as yet unpublished theses, on long-term phenology monitoring from India, and a few preliminary insights from the same.

BOX 1
Long-Term, Large-Scale Monitoring of Plant and Animal Phenology through Citizen Science

Across the world, biodiversity information is generated not only by ecologists, but also by naturalists and enthusiasts. The collection, curation and classification of information about the natural world by volunteer participants is called 'citizen science', alternatively termed 'public participation in scientific research'. Citizen science is particularly useful in addressing research questions that require the collection of large-scale and long-term data, such as country-wide monitoring of plant and animal phenology. In India, two citizen science programmes - Bird Count India and SeasonWatch - are working to generate such large-scale and long-term data on various aspects of birds, including migration and on tree phenology, respectively. Seasonal patterns in bird (Figure 3) and plant (Figure 4) phenology are emerging from these efforts, which are being continued in the long-term to understand bird and plant phenological responses to future climate change. To date, over 7500 trees have been registered with SeasonWatch and over 1.9 lakh observations have been contributed on the phenology of these trees. As the programme expands, better species-wise sample sizes and repeated measures on registered trees will allow one to model the underlying diversity of tree phenological response as a function of environmental factors, and eventually predict phenological change with future climate change.

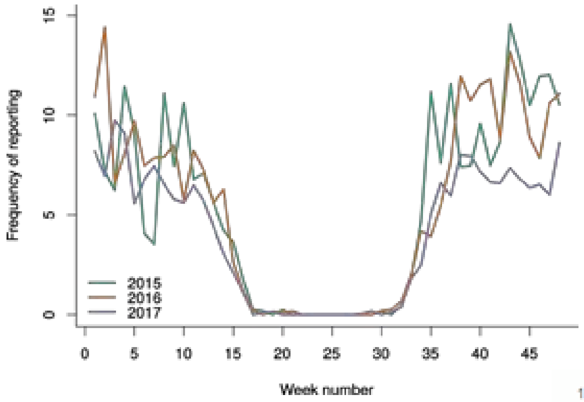
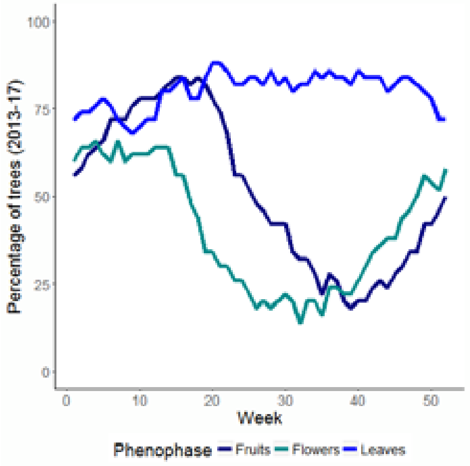


*Figure 3: Frequency of reporting of a winter migrant, the Grey Wagtail (*Motacilla cinerea*) from Karnataka, Kerala and Tamil Nadu, on the eBird-India platform (managed by Bird Count India). The frequency of reporting is the percentage of bird lists that report this species. Note that although winter reporting rates are variable between years, the timing of arrival and departure is remarkably consistent across the three years.*

Figure 4: Average seasonal variation in proportion of Artocarpus heterophyllus *trees with mature leaves, flowers and fruits, the most observed species of tree under SeasonWatch. The data presented here are summarised from the years 2013 to 2017. On average, mature leaves seem to show no seasonality, while flowering and fruiting seems to peak between week 10 and 20 of the year.*



CASE STUDY 1: PLANT PHENOLOGY AND CLIMATE IN RISHI VALLEY, ANDHRA PRADESH

Rishi Valley is a semi-arid tropical scrubland (700 m ASL) located along the Eastern Ghats on the Deccan plateau, located in the southern Indian state of Andhra Pradesh. The climate of the valley can broadly be classified into 4 periods: a cool dry period from December to February, a hot dry period from March to May, the south-west monsoons - the warm-wet period from June to August, and the north-east monsoons - the cool-wet period from September to November. The temperature can be as low as 8ºC, and as high as 41ºC in summer. Rainfall is scanty and erratic with an average rainfall of around 800 mm annually.

Quader et al. (unpublished) have been monitoring vegetative, flowering and fruiting phenology of 40 individuals in 18 different species in the landscape since December 2007, every fortnight. The species include 12 trees and 6 shrubs. The 12 tree species include 3 native *Ficus* species, 6 native and 3 non-native species. Of the shrubs, only one - *Lantana camara*, is a non-native and invasive species.

Sixteen of the 18 species shed their leaves in the cool dry season. Of the 16, all the shrubs and one tree had prolonged deciduous periods of complete leaflessness as compared to the remaining trees that had shorter or no period of complete leaflessness. The duration of deciduousness varied considerably between years.

Only one species showed no seasonality in leaf flush. Three species showed partial seasonality. All others had a dormant period after the monsoons, through the cooler months and flushed leaves during the hot dry periods. All species continued to flush leaves through the monsoons and were either extended or bimodal, with peaks coinciding with the two monsoons.

All flowering species showed seasonality. Eleven of 15 species put out buds soon after flushing leaves during the warm dry summer. Four of these 11 species had short pronounced flowering periods, while the remaining had extended flowering that continued through the monsoons. Only one species flowered exclusively during the dry months. The remaining three species flowered predominantly during the north-east monsoon.

Ficus species did not show seasonality in fruiting. While all species were seasonal in flowering, with pronounced durations, fruiting was more varied. Most species showed presence of fruit for extended periods of time. Eight of the summer flowering species held fruits through the monsoons, of which 2 continued through the cool dry periods. The late flowering species all developed fruits during the late monsoons, and persisted through the cool dry period.

With over 10 years of monitoring, we are now able to understand the climatic drivers of these phenophases and accurately model phenological responses to climate. Logistic modelling of leaf flush as a response to moisture stress of two shrub species (Figure 5) not only reveal clear correlations but also show differential responses to the climatic variables. The invasive *Lantana camara* flushes leaves slower on release of moisture stress as compared to the native *Erythroxylum monogynum* species, which has a steeper slope.

Similar models for all the monitored species show that both vegetative and reproductive phenophases in shrubs are strongly driven by precipitation and therefore, show high year to year variation in timing and effort.

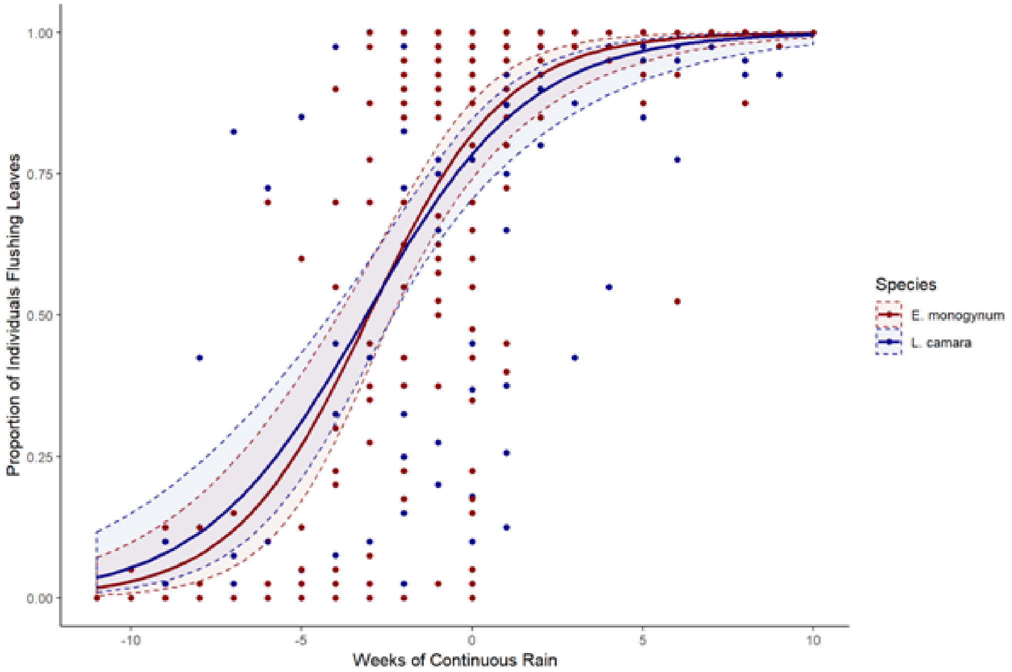


*Figure 5. Logistic model of leaf flush of two shrubs (*Erythroxylum monogynum *and* Lantana camara*), over 212 fortnights, as predicted by availability of moisture. Positive values on the x-axis represent continuous weeks of rain above 8 mm and negative values depict continuous weeks of drought or lack of rain above 8 mm. The points depict the actual observations. The solid lines trace the best fit line as predicted by the logistic model for each species and the coloured regions around the lines show the 95% confidence intervals around the estimates.*

The onset of both flowering and leaf flush in shrubs correlate with early summer showers and seem to require moisture stress reduction to put out these phenophases. Trees are hardier and more consistent in their timing of leaf flush and flowering between years. Smaller trees as well seem to require release of moisture stress to put out their vegetative phenophases. Reproductive phenophases of all trees as well as leaf flush in the larger trees correlate to either irradiation, photoperiod or temperature; all three of these climatic variables are strongly correlated with each other, making it hard to deduce the actual climatic driver. While effects of climate change on phenology are still hard to infer in this landscape, we now have valuable baseline information as well as a predictive framework to assess future climatic scenarios that will prove invaluable for both conservation and management.

Case Study 2: Tree Phenology, Dispersal and Climate in Pakke, Arunachal Pradesh

Datta (2001) described the seasonal and annual variations in flowering and fruiting patterns of 165 tree species. The presence/absence of flower, unripe and ripe fruit was recorded monthly from February 1997 to July 2000 in 1899 trees in twenty-one 0.25 ha plots in Pakke Wildlife Sanctuary, a tropical semi-evergreen forest in Arunachal Pradesh. Community-wide flowering and fruiting patterns, and of anemochorous and zoochorous species were examined graphically. Climatic factors such as rainfall over 40 months, total rainfall in the previous 6 months, rainy days, and monthly minimum and maximum temperature were correlated with number of species and percent

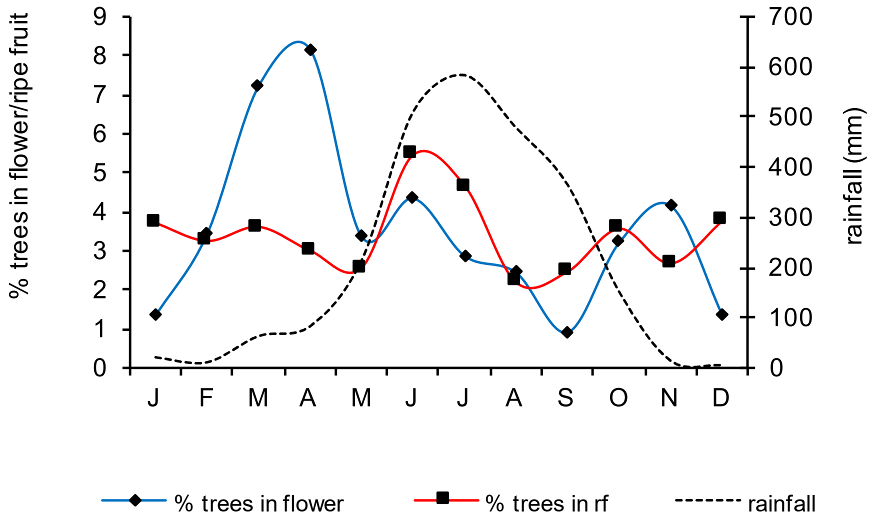


Figure 6. Community-wide annual flowering and fruiting patterns (1997-2000) in Pakke Wildlife Sanctuary, Arunachal Pradesh with rainfall. n = 165 tree species, 1899 trees

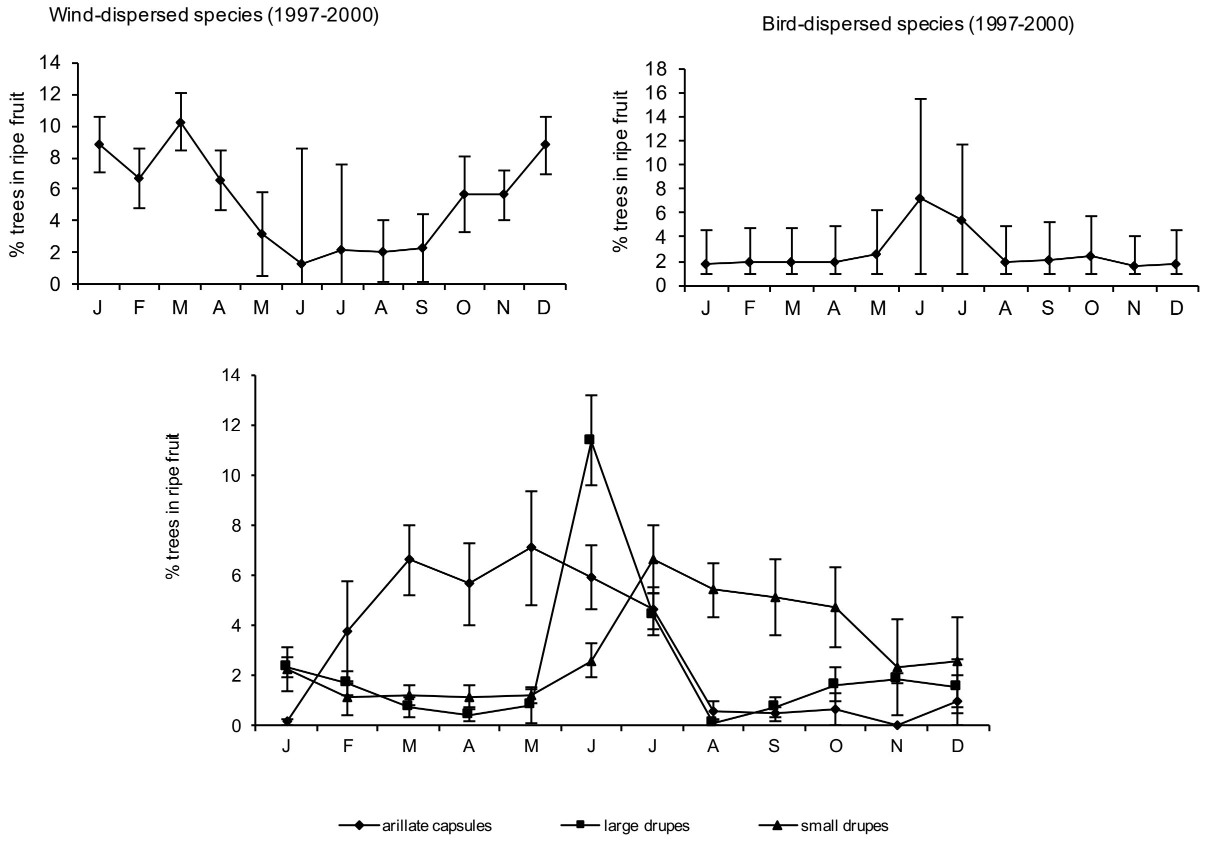


Figure 7. Seasonal and annual fruiting patterns of (a) wind and bird dispersed species, and (b) arillate capsular fruits and drupes in Pakke Wildlife Sanctuary, 1997-2000.

trees with flower and ripe fruit. Sixty-four percent (106 species) of tree species were animal-dispersed, 12% (21 species) were wind-dispersed, while the dispersal mode of 38 species could not be established. Of the animal-dispersed species, 57 were mainly bird-dispersed (Datta and Rawat 2008).

The main peak in community-level flowering was in March-April (dry hot season) with 8% of trees in flower, with smaller spikes (4% of trees) in June and November (Figure 6). Fruiting peaked between May and July (Figure 6). The quantum of flower and fruit availability was low with 4-8% of trees in flower/fruit even during peak flowering/fruiting. Fruiting declined from September to January (post-monsoon/winter).

Flowering of wind-dispersed species was bimodal, occurring during dry months, February to April and October to December, while bird-dispersed species flowered throughout the year. For 15 wind-dispersed species, the number of species in flower in each month (rs= -0.395, $p < 0.05$ with rainfall; rs= -0.447, $p < 0.01$ with rainy days; rs= -0.349, $p < 0.05$ with minimum temperature) and percent of total trees in flower in each month (rs= -0.416, $p < 0.01$ with rainfall; rs= -0.460, $p < 0.01$ with rainy days; rs = -0.384, $p < 0.05$ with minimum temperature) were negatively correlated with rainfall, rainy days and minimum temperature. Fruiting was also negatively correlated with the same variables.

The flowering patterns of 35 bird-dispersed species were not correlated with rainfall, rainy days, minimum and maximum temperature. The number of species in flower (rs= -0.539, $p < 0.01$) and percent trees in flower (rs= -0.579, $p < 0.01$) were negatively correlated to total rainfall in the previous 6 months. Percent trees in fruit was positively correlated with rainfall (rs= 0.306, $p = 0.056$) and rainy days (rs= 0.343, $p < 0.05$). Fruiting was negatively correlated to total rainfall in the previous 6 months (rs= -0.379, $p < 0.05$).

Fruiting of wind-dispersed species was bimodal peaking in drier months, while the fruiting peak of bird-dispersed species was unimodal during the wet season (May-July) (Figure 7a) with high variability between years. Fruit availability of bird-dispersed species was more uniform, which suggested that there is staggering of bird-dispersed species throughout the year that may be driven by extra-climatic conditions. Species of Meliaceae and Myristicaceae with large-seeded arillate fruits ripened from March to May, while fleshy drupes of Lauraceae, Annonaceae and others ripened between July and December (Figure 7b). Peak fruit abundance of bird-dispersed species coincided with the breeding season of resident frugivores. Species with smaller fleshy drupes were available during winter, coinciding with the arrival of migrants. While tree reproductive phenology may be primarily influenced by climate, within that optimal period, bird-dispersed species appear to show staggering in fruiting schedules that suggests support for the competition avoidance hypothesis (Terborgh 1990) which predicts that fruiting schedules of tree species that share common dispersers should be staggered to avoid competition for dispersers.

Given that minimum temperature and rainfall patterns are linked with flowering and fruiting, any future changes in climate may have consequences for the timing, duration and quantum of flower production. Most species in this system are insect-pollinated and climate change may have effects on pollinator abundance, which would affect fruit set and maturation. This is likely to have downstream consequences for the food availability and breeding cycles of several bird species.

CONCLUSION

Seasonality is ubiquitous across the globe, including in most of the tropics, which are often incorrectly described as 'aseasonal'. Abiotic factors, like temperature, precipitation and irradiation, show seasonal changes across the year, and biotic components of ecosystems are adapted to match their growth and reproduction to favourable seasons. In general, primary producers (plants) have evolved according to seasonality in abiotic factors, and animals at higher trophic levels have evolved to match seasonality in the trophic levels below. Seasonality of plants and animals in an ecosystem are thus tightly linked together. Since climate change affects seasonal changes in various abiotic factors, plants (and therefore) animals will need to adjust phenology accordingly, or face a mismatch between climate on the one hand, and growth and reproduction on the other. Phenological mismatches may result in population changes in individual species and consequent alterations of trophic webs. Understanding the mechanisms underlying phenological patterns and being able to predict consequences of changing climate is therefore essential to forecast how natural ecosystems will respond to climate change. Although this review focuses on phenology in natural systems, similar impacts in agricultural and horticultural systems (for example, mediated by pollinators) will also have profound consequences for human well-being.

Shorea robusta - *Buxa Tiger Reserve, West Bengal (Photo: J.M. Garg; Wikimedia Commons)*

The detailed and long-term work done in temperate regions gives some insight into the effects of climate change on phenology, and possible trophic consequences. A broad conclusion from studies of plant and animal phenology is that increasing temperature over timespans of years to decades is associated with earlier phenophases, leading to a rate of advance in the onset of these phenophases by 2.8 days per decade (Parmesan 2007), on average. Less work has been done on potential consequences down the trophic chain of these phenological changes, but there are a few well-described examples of resultant decoupling of phenology across trophic interactions. Community-level outcomes of phenological changes induced by climate change are still poorly understood.

In the tropics, the comparatively little work that has been done suggests a more complicated picture. Phenology of tropical plants appears to be affected by precipitation and solar irradiance, along with (in some cases) temperature. The precise outcomes are inconsistent, and depend on whether, for example, precipitation becomes more irregular (possibly leading to a longer growing season) or decreases overall (with the opposite effect). Together with the greater predictive uncertainty of climate models for tropical regions, this makes it difficult to predict and generalise phenological changes in the case of climate change. Trophic consequences and ecosystem-level changes in the tropics remain unexplored.

Much of what we know about the causes and consequences of phenological changes comes from long-term studies (e.g. 10 or more years). By contrast, most phenology studies in India are 2-3 years long. Over these timescales it is possible to describe phenological patterns, but difficult to uncover the biotic and abiotic factors underlying variation in phenology. For a better understanding of plant phenology in India, two opportunities must be pursued: (1) re-surveying locations of prior phenological work to uncover possible changes in phenology, and their relationship with underlying climate, and (2) long-term continuation of current phenology projects as well as the initiation of new projects of this kind. These efforts should ideally lead to better coverage in terms of geography, life-form and ecosystems across India, and include systems thought to be most vulnerable to climate change, such as the Himalaya. A number of research groups are currently working on long-term phenology studies, and a loose network of such efforts would help in coordinating research, identifying and filling gaps in spatial coverage, building capacity for such work, and synthesizing resultant patterns. While such long-term research projects are often in-depth and focussed on specific locations, another avenue for long-term phenology data can be from citizen science projects that can potentially provide broad spatial coverage to supplement understanding of current patterns and future change. Yet another nascent mode of exploration, is the use of remote sensing techniques to detect phenological changes at large spatial scales over time, and to correlate the same with ambient weather parameters (e.g. Prabakaran et al. 2013).

Research on phenology from India is so far poorly represented in the global understanding of tropical phenological patterns and responses to climate change. With some planning, coordination, and collaboration between people/institutions, it is hoped that we can obtain a more comprehensive understanding of phenological patterns and responses to climate change in the future.

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Bird Migration and Climate Change

Suhel Quader

*Grey-headed canary-flycatcher (*Culicicapa ceylonensis*), Nilgiris, south India (Photo: Sameer Jain)*

Bird migration is a global phenomenon in which large numbers of species and individual birds move over hundreds to thousands of kilometres seasonally. In North America alone, over 4 billion birds migrate annually (Dokter et al. 2018). These seasonal movements are thought to occur largely to track seasonal changes in resource availability, primarily food. Proximate cues that trigger migration include changing daylength and temperature, as well as food availability. Since changing climate can influence both the evolutionary reason for migration (food) as well as some of the proximate cues (e.g. temperature), there has been much interest in understanding possible impacts of climate change on bird migration.

A large body of work has sought to assess changes in timing (i.e. the phenology) of migration. An overall pattern is that the timing of spring migration (returning to breeding areas) in the northern hemisphere is clearly becoming earlier. For example, summarising a number of studies, Walther et al. (2002) concluded that spring migration has advanced by 1.3–4.4 days per decade in Europe and North America. However, the timing of return migration to nonbreeding grounds appears to be variable and context-dependent (Jenni and Kéry 2003). Attempts have also been made to predict the magnitude of phenological change and downstream consequences. For example, if birds respond to local weather conditions, then differences in the rate of warming between breeding grounds (further from the equator and therefore showing greater warming rates) and non-breeding grounds are expected to lead to a 'phenological mismatch'. In such a situation, birds return later than optimal to breeding areas, with greater effects on species that migrate further (Jones and Cresswell 2010). Such effects may be counterbalanced by changes in migration distance. Evidence from birds ringed in the Netherlands suggests that migration distances have been decreasing over time and in a manner that is correlated with temperature, potentially allowing species to better predict onset of spring in breeding areas (Visser et al. 2009). Not all migration is over long distances and across latitudes; a number of species show short-distance migration, particularly across elevations in montane regions. There is some evidence that the timing of elevational migration is also affected by climate change (Inouye et al. 2000), but this phenomenon is much less studied than is long-distance migration.

Migration phenology and distance can thus be used as barometers of climate change. But it has also been suggested that phenological mismatches may have long-term population consequences and therefore conservation implications. For example, European bird species that did not change the timing of their migration were also those whose populations declined most dramatically in the period 1990-2000, compared to those species which showed advanced spring migration (Møller et al. 2008). This implies that while some species may be plastic (or adaptable) enough to respond suitably to the climate changing within certain bounds, those that are unable to adjust appropriately will face declines and possible extinction in the years and decades ahead.

By its nature, the impact of climate change can be understood only through long-term studies and datasets. While some of these come from multi-decadal work at field stations and designated monitoring sites, a large fraction of assessments rely on data collected through citizen science (e.g. Hurlbert and Liang 2012; Cooper et al. 2014).

In India, migration studies have focussed on ringing, tagging and satellite tracking to elucidate the spatial movements of migratory birds (Balachandran et al. 2018) and on migratory birds as a possible vector for zoonoses. Very little work has been done on assessing migration timing (and possible changes), either at long-term observatories or using information from citizen science. In the absence of field stations or observatories

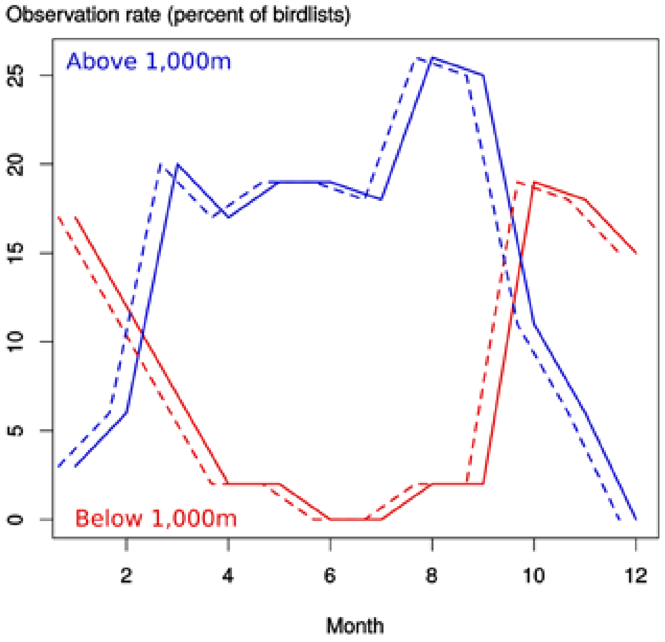

*Figure 1. Timing of elevational migration of grey-headed canary-flycatcher (*Culicicapa ceylonensis*) in Uttarakhand. During the summer months, this species breeds at higher altitudes in the Himalayas. Their movements to lower elevations starts in September-October, which is when they are reported at high frequency below 1,000m. Spring migration back to the breeding grounds begins in February and is complete by March. The dotted lines indicate a hypothetical future shift in elevational migration in which all movements are advanced by 10 days. This graph uses roughly 4,000 records of the species from over 25,000 bird checklists from Uttarakhand, uploaded to the bird listing platform eBird (ebird.org/india).*

*Pied cuckoo (*Clamator jacobinus*) in Coimbatore, Tamil Nadu - the harbinger of the monsoon (Photo: Sameer Jain)*

in India that gather data on migration timing from capture or observation of migratory species using some manner of constant effort, two examples based on data generated from citizen science may prove instructive.

The pied cuckoo (*Clamator jacobinus*) is a species that migrates from Africa to central and northern India (southern India has a resident population). According to widespread folklore, this species (called 'chaatak') heralds the onset of the monsoon. Data generated from birdwatchers uploading their first sightings of the season to the online platform MigrantWatch (migrantwatch.in) provides support for this common belief. In all four years examined, earliest reports of this species were seen in advance of monsoon arrival, and arrival preceded the monsoon by a greater number of days in regions of late monsoon onset (MigrantWatch 2013).

A second example illustrates the power of the vast amounts of data generated by citizen science to set baselines against which future changes in migration can be assessed. Since 2014, , the umbrella group Bird Count India (birdcount.in) has been encouraging birdwatchers to help document and monitor Indian birds. Until now, more than 12,000 birdwatchers have uploaded over 11 million observations of birds in India to the bird reporting platform eBird (ebird.org/india). The seasonality of migration (e.g. arrival and departure; or timing of passage migration) to different regions of the country is, as a consequence, now described in sufficient detail to be able to assess possible changes over future years and decades. As an example of such a baseline, consider the elevational migration of the grey-headed canary-flycatcher (*Culicicapa ceylonensis*) in the Himalayas of Uttarakhand state. Based on over 3,000 observations of the species from 22,500 bird lists, the seasonal pattern becomes clear (Figure 1).

Nearly 300 bird species migrate to and from India (or pass through) every year. For several, India is home to almost the entire global population in the non-breeding season, and we are therefore custodians of these species for a good part of the year. Our understanding of the effects of climate change on these movements, however, is rudimentary. To improve this state of affairs, a small number of actions are likely to have a large impact. A key component is to set up long-term observatories in sites across the country, where constant-effort data are collected. These data should ideally include both observations (e.g. from transects or point counts) as well as captures (e.g. mist-netting for ringing and release). Information on migration generated in this way can be supplemented by large-scale aggregation of data collected through citizen science, whether through relatively unstructured means (e.g. Figure 1) or targeted and seasonal counts at particular sites, along the lines of the Asian Waterfowl Census. Open sharing of information generated in these efforts will enable new ideas and analyses that are not possible when data are not made publicly available. These few actions (setting up long-term observatories, encouraging citizen science, requiring data sharing) will go a long way in generating a better understanding of how bird migration is responding to climate change.

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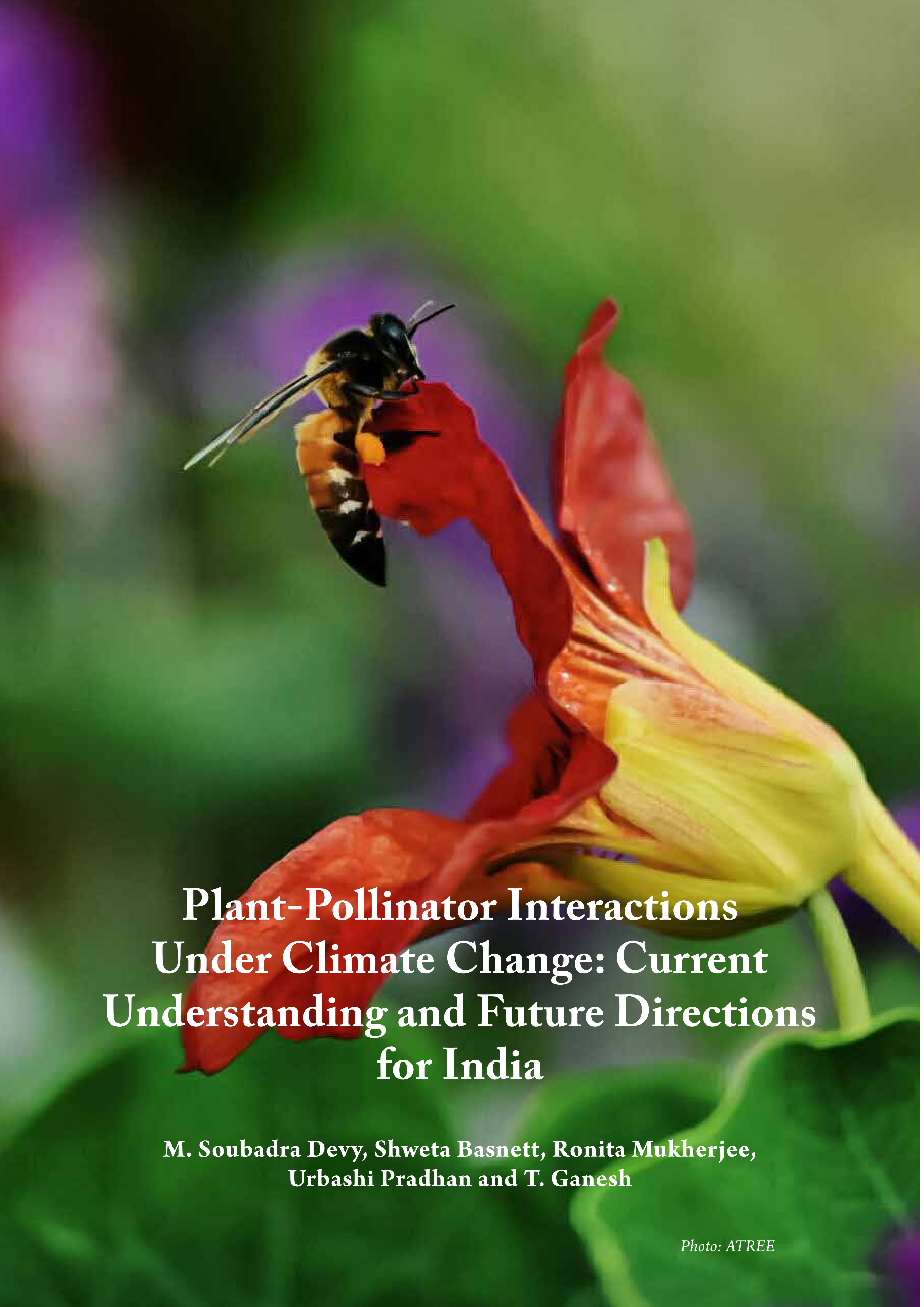

Plant-Pollinator Interactions Under Climate Change: Current Understanding and Future Directions for India

M. Soubadra Devy, Shweta Basnett, Ronita Mukherjee, Urbashi Pradhan and T. Ganesh

Photo: ATREE

INTRODUCTION

Plant-pollinator interactions not only mutually benefit plants and animals but also contribute to human well-being through the yield of food crops, and indirectly through the functioning of many natural ecosystems (Nabhan and Buchmann 1997; Costanza et al. 1997; Klein et al. 2007). About 87% of the estimated species of flowering plants are pollinated by animals (Ollerton et al. 2011), and about 35% of crops grown globally depend on animal pollination (Klein et al. 2007). There is growing evidence of the linkage between greenhouse gas emissions (through human use of fossil carbon) and global change (IPCC 2007) and an urgent need to understand the consequences of this on plant-pollinator interactions, which are indispensable to the functioning of ecosystems.

Taxon-based species extinctions have received enormous attention and species co-extinctions have also received attention (Koh et al. 2004). Koh et al. (2004) also emphasize that loss of species that co-exist and interact such as plant-pollinators, would mean a loss of irreplaceable evolutionary history, which is often insidious. In recent times, plants and their interacting pollinators have been facing risks both at the local scale through pesticide use (Paini 2004; Shavit et al. 2009; Whitehorn et al. 2012; Doublet et al. 2015) and disease (Sammataro et al. 2000), and at the global scale from habitat loss (Fortuna and Bascompte 2006; Aguilar et al. 2006; Potts et al. 2010), altered land-use (Kremen et al. 2007; Foley et al. 2007) and climate change (Inouye 2008; Gilman et al. 2010). Further, these global scale risks can have feedbacks at the local scale (Box 1). Studies suggest that global warming, along with habitat loss and fragmentation, can cascade into the large-scale extinction of interactions which are responsible for key ecosystem services, such as pollination of plants (Kearns et al. 1998; Walther et al. 2002; Thomas et al. 2004; Biesmeijer et al. 2006).

More recently, there has been growing concern about the loss of pollinators (Kearns et al. 1998; Steffan-Dewenter et al. 2005), particularly following the 'colony collapse disorder' in temperate regions, which was characterized by a huge number of dying colonies (VanEngelsdorp et al. 2009). However, knowledge of climate change effects on plant pollinators are limited, and there is very little empirical evidence on how this will affect ecosystem services (Kremen et al. 2007). Studies – using historical data as well as using modelling approaches – on different aspects of climate change impact on pollination are emerging, but are mostly biased towards temperate regions (Biesmeijer et al. 2006; Hegland et al. 2009; Potts et al. 2010). Climate change has been predicted to increase fluctuations in rainfall and temperature, making climate change scenarios even more conspicuous (Karl and Trenberth 2003). Most studies on pollination deal with the important role of temperature on the interactions between pollinators and plants (Lobell et al. 2012), although many other environmental cues such as rainfall anomalies associated with climate change could also influence such interactions (Minckley et al. 2013). While there is still a gap in the prediction of climate change at specific regional scales in India, studies of past patterns of climatic data show that the northern parts of India tend to have sharper increases in temperature and more precipitation – in the form of infrequent heavy deluges, associated with local flooding becoming more common in the Western Ghats, the Himalayas and the plains of India (Dash and Hunt 2007). However, climate change is more apparent in the Himalayas compared to other regions in India, and local communities have perceived remarkable changes over the last few decades (Shrestha et al. 2012).

Studies in India have reported a decline in pollinators due to various factors such as habitat loss and adoption of faulty agricultural practices without having prior knowledge about basic plant-pollinator interactions (Sinu and Shivanna 2007; Basu et al. 2011). Studies designed to understand climate change effects on plant-pollinator interactions are just emerging in India (Basnett et al. 2018, under preparation; Mukherjee et al. 2018, under preparation). However, studies which monitored plant-pollinator interactions in the long term have also picked up indirect evidence of the likely consequences of climate change (Ganesh et al. 2017). Here, we review the various aspects and approaches of studies that have been carried out to examine the effect of climate change on plant-pollinator interactions globally, and also present a few key case studies on pollinators from India, from different biogeographic regions. Finally, we present a framework which can help examine and monitor the effect of climate change on plant pollinators in India in a more comprehensive way, and develop an adaptation strategy. This is particularly important for food and agriculture, and also to understand the mechanism of adaptation in natural systems.

INFLUENCE ON FLORAL TRAITS AND ITS CONSEQUENCES

Floral traits play an important role in the patterns of plant-pollinator interactions (Fenster et al. 2004). An experimental study was designed to look at the effect of elevated CO_2 and drought on visual traits such as pigmentation and floral display, floral rewards such as nectar and pollen, and olfactory traits such as volatile organic compounds which play a critical role in flower fidelity and averting interspecific pollen transfer (Glenny et al. 2018). In this experiment, four species of forbs were subjected to elevated carbon and compared with ambient carbon, and also to drought compared to normal water availability. The elevated carbon enhanced visual cues and volatile organic compounds (VOCs), which resulted in higher visitation rates. Drought decreased visual traits but increased VOC emissions, which had a negative effect on visitation.

This study demonstrated that climatic variables associated with climate change have variable effects on crops. Plants under drought stress might reduce flower numbers, size, nectar volume and sucrose – all of which are cues to attract pollinators (Alqudah et al. 2011). If drought is drastic and widespread spatially, low floral output can lead to low fruit-set, and this can have a cascading effect in forest ecosystems – particularly in tropical forests, as it can result in fruit scarcity for the frugivorous community of the forest (Terborgh 1986, also see Box 2). Reduction of flower numbers of pollinator-dependent crops during droughts can drastically bring down yield (Zimmerman and Pyke 1988; Lee and Felker 1992; Campbell 1996, see Box 1 for an Indian case study).

PHENOLOGICAL MISMATCH OF PLANTS AND POLLINATORS

Environmental factors associated with climate change have the potential to affect the phenology of both plants and pollinators (also see Ramaswami et al. this volume). Phenology in temperate regions and high latitudes is known to be more strongly influenced by day length in combination with rising temperatures (Ranjitkar et al. 2013; Li et al. 2016), which might trigger the initiation of physiological activity after winter dormancy at higher latitudes. In contrast, the aseasonal tropics are known to have limited annual variation and other kinds of

environmental signals that could serve as reliable indicators of the season and/or as proximate releasers of physiological activity (van Schaik et al. 1993). For instance, temperature might act as a cue for flowering, while changing rainfall patterns (in terms of timing and also intensity) interfere with plant-plant interactions (see Box 1 for an Indian case study).

India has diverse ecosystems – the seasonally dry tropical forests which occupy a significant part of central India, the Western Ghats along the western coast with unique mid-elevation wet evergreen forests and the Himalayan forests towards the north, ranging from tropical moist deciduous forests (300–900 m) to temperate to dry alpine scrubs (above 4,000 m) (see Champion and Seth 1968). These ecosystems represent diverse climatic regimes, and along with this, there is the monsoonal effect which is also predicted to be influenced by climate change (Gergis and Fowler 2009). The response of plants and their interacting pollinators from these ecosystems could also be variable.

Much of the knowledge of climate change effects has come from phenological studies (Primack et al. 2004; Miller-Rushing et al. 2007; Hart et al. 2014; CaraDonna et al. 2014; CaraDonna and Inouye 2015), and of late, there has been a surge in interest on phenological responses to climate change and interacting species of pollinators (Hegland et al. 2009; Bartomeus et al. 2011; Forrest and Thomson 2011; McKinney et al. 2012). Mismatch in phenology of plants and their pollinators will reduce their overlap habitat either temporally or spatially, and this can result in partial or complete decoupling (Stenseth and Mysterud 2002; Visser and Both 2005), leading to poor fruit set and recruitment. There have been speculations of mismatches in plant-pollinator interactions (Harrington et al. 1999; Visser and Both 2005; Parmesan 2006), but very few empirical studies that report decoupling of these interactions exist.

Memmott et al. (2007) worked on a simulation of global warming-influenced plant-pollinator networks, where they applied phenological shifts between 17 and 50% and predicted that pollinator species suffered from disruption of food supply due to temporal mismatch. Benadi et al. (2014) have argued that many pollinators may have greater dietary flexibility than was assumed by Memmott et al. (2007), and that they would adopt new food sources in dire situations. They support their argument with substantial evidence that plant-pollinator linkages are flexible. Various types of observational data (based on long-term and multi-site observations as well as more anecdotal evidence) point to phenological shuffling regularly occurring at a low level, with overlap between particular pairs of plant and pollinator species increasing or decreasing depending on climatic conditions. Therefore, there may not be any dramatic disruptions with regard to plants or pollinators – they may not suffer a complete loss of interaction partners (Bartomeus et al. 2011).

Most of the evidence on decoupling have been built on historical data (Bradley et al. 1999), long-term monitoring sites (Inouye and McGuire 1991) and even citizen science efforts (Hurlbert and Liang 2012). Unfortunately, India has very few long-term monitoring sites. While most of them focus merely on plant phenology, there are a few sites which monitor the phenology of plants and pollinators (Siddappa et al. 2001; Ganesh et al. 2017). However, the alternate approach of conducting experiments during years of climate extremes and normalcy helps understand the response of these systems (Box 1).

BOX 1
Response to Rainfall Extremes

The concept of 'ecological fitting' was first proposed by Dan Janzen in his seminal paper of 1985. In his theory, he argued that the evolution of novel species interactions could be explained independently of the assumption of coevolution. Ecological fitting is a form of natural selection where only those interactions which provide fitness benefits are retained in the scenario of novel species interactions. Such interactions can occur due to processes like colonisation, invasion, introduction to a new environment, or due to a sudden shift in the present environment. This process does not require long-term association between two species, which is a necessary condition for coevolution. However, this phenomenon does require the presence of sufficient natural variation in order to increase its probability. Interestingly, the origin of novel species interaction is increasing in frequency owing to human interventions – through species introductions and human-induced climate change.

Agricultural yield in India, like most other developing agrarian countries, depends heavily on rains. Decades of research show strong dependence of the majority of horticultural crops on rainfall volume (Aizen et al. 2008). We wanted to examine the impact of climatic variation (rainfall) on plant and pollinator components that influence the yield of a horticulturally dominant crop of southern India, Chayote squash. Standard pollinator-exclusion (bagging experiments) and field observations across multiple sites gave us an idea about the pollination biology of the selected study species. In order to understand the impact of rainfall variation on crop yield, we conducted the study over two years with varying rainfall amounts (normal and drought year). We hypothesised that rainfall decline would impact the final yield by affecting the plant, pollinators, and their interaction.

Alqudah et al. (2011) found that rainfall shortage affects crop pollination by affecting ovary development, pollen grain sterility, nectar volume, flower attractiveness and seed set. Rainfall decline had also been shown to shift forest phenology (Peñuelas et al. 2004) and floral abundances (Thomson 2016). Devoto et al. (2005) showed that variation in rainfall impacts pollinator distribution and abundance. Besides, any sudden climatic shift can lead to a change in pollinator community and plant-pollinator interactions across the globe (Hegland et al. 2009), and rainfall decline has been found to cause pollinator extinction, as in the case of dioecious fig species of Borneo (Harrison 2001).

However, in biodiversity-rich countries like India, owing to the presence of multiple native pollinators, it is probable that such a decline of a single pollinator species is compensated by other native species. Naeem and Li (1997) in their seminal paper proposed such an ecosystem-stabilising mechanism known as 'density compensation', wherein in the case of a critical species loss, biodiversity (in the form of another species) can compensate for its functional loss. This theory highlights the importance of maintaining diverse pollinators, as some pollinators may be able to cope better with climatic fluctuations and sustain yield in the face of climate shifts. Among the key indicators of pollination efficacy, fruit-to-flower ratio is expected to show a significant outcome under declining pollinator visitation (Ne'eman et al. 2009).

Pollinator (Apis dorsata) visiting flowers of Chayote squash

We thus speculate rainfall decline will potentially impact crop yield by low floral output or a drastic shift in the pollinator community. These, in turn, might impact plant-pollinator interactions by altering the fruit-to-flower ratio. We also speculate that surrounding landscapes – small patches of semi-wild areas or large protected areas – will be crucial for the sustenance of pollinator flow (Bodin et al. 2006).

In the present state of climatic fluctuations, due to rapid development and urbanisation, agriculture – one of the principal occupations of the majority of the commons – is at stake. Our study reinforces the need for studies dealing with the basics of agricultural crop dynamics to come up with sustainable policies to deal with current climatic shifts, and preserve agro-production without destroying natural biodiversity.

*Lion-tailed macaque (*Macaca silenus*) eating* Cullenia *flowers (Photo: T. Ganesh)*

Asian forests are bestowed with not less than five species of *Apis* or honey bees (Otis 1996) which serve as 'super-pollinators' of many wild and cultivated species. There is evidence that points to the system pollinated by *Apis* or the honey bees being resilient as many species forage on a single species of plant (Oldroyd et al. 1992). However, we need long-term data to understand directional change from various sites of India to completely understand climate change-related responses (see Box 1).

Changing Climate Conditions and Keystone Species

Fig Wasps and the Fruit-Eating Community

Figs (*Ficus* species) are one of the most diverse and ecologically important genera (Lambert and Marshall 1991) they have been known to play the role of a keystone resource. Their asynchronous or aseasonal fruiting pattern implies that a part of the population produces fruits throughout the year, thereby becoming a keystone resource for many frugivorous organisms during periods of fruit scarcity (Terborgh 1986). Figs also have very species-specific pollinating wasps (Hymenoptera: Agaonidae) - every fig species has a unique wasp species which has co-evolved with it (Harrison 2000).

About 89 species of figs have been reported from all over India (Chaudhary et al. 2012). However, not all wasps associated with them have been recorded (Rajan personal communication). Harrison (2000), who has worked extensively on figs, has reported local extinctions of fig wasps during severe droughts – leading to fruit abortions – and links it to El Niño Southern Oscillation (ENSO) events. He warns of an increase in the frequency of such drought events in the coming years. The Indian monsoon is strongly influenced by ENSO events, and there are predictions of more frequent droughts in the coming years due to the warming of the planet (Gergis and Fowler 2009). Krishnamani and Kumar (2018) attribute the rarity of the lion-tailed macaque (*Macaca silenus*), a highly endangered species, to the distribution of its food plants - mainly comprising *Ficus* species. If there is an increase in ENSO-related drought events in India (Gergis and Fowler 2009) it is likely that fig wasps will go extinct, and this can have a cascading effect on fruit-eating communities, including that of the lion-tailed macaque.

Cullenia - The Woes of Summer Rain'

Cullenia exarillata ('vedipla' in Tamil/Malayalam), a canopy species, is characterized by a unique pollination system. *Cullenia* produces flowers directly on its woody branches. These flowers are eaten by several canopy mammals and birds, some of which also help in their pollination. The flowering season of *Cullenia* coincides with the period of fruit scarcity in forests, and hence its flowers become important keystone resources for arboreal mammals.

Our observations of *Cullenia* flowering revealed that, in degraded and fragmented forests, there are fewer visits by arboreal mammals to the flowers, which sometimes leads to fewer fruits. This is often due to the presence of unattended flowers, which are laden with sucrose-rich nectar. These develop fungal infections, leading to the flowers rotting on the branch, and this could be exacerbated if rainfall occurs during the flowering period. To test the effect of unseasonal rains during the dry season, we simulated rain over the flowers through a sprayer and tagged these flowers (and others that had not been sprayed), and followed up to fruit set. Not surprisingly, the 'watered' flowers developed a fungus in most cases. As a result, no visitors came and no fruits were produced. However, more long-term work is needed to understand how consistent these 'effects' are.

Palaquium - A Magnet Species

Apis dorsata (rock bee), is a key pollinator of plant species in the Western Ghats. It is also an elevational migrant which tracks the flowering phenology of tree species which shift from lower elevation dry forests (at 400 m) to wet evergreen forests (at 1200 m) in the southern Western Ghats, India. Our long-term phenological studies (1991-2015) has shown that bee arrival in the rainforests is determined by the flowering of *Palaquium ellipticum*, a canopy tree species (Devy and Davidar 2003). The flowering period coincides with the pre-monsoon period in May, before the onset of the southwest monsoon; the rock bees are not deterred from visiting flowers by the occasional drizzle. *Palaquium* is the only nectar source and occurs in high density in the site and also flowers annually, while the other food-plant species that flower ahead of and around the period are either very low in density or flower supra-annually (unpredictable, and flowering intervals could be widely spaced between 3 to 12 years). Some of these are visited by *Apis cerana*, a resident species, which is present in very low density in the site. *Apis cerana* is also an erratic visitor to many of these species. Thus, the rock bees play a disproportionate role in the pollination of many species. Many tree species which occur in very low density and flower during the period of *Palaquium* flowering also derive benefits from rock bee visits, making *Palaquium* a 'magnet species' - a species that facilitates pollinator interaction with species which may not be able to attract them independently (Laverty 1992).

*Rock bee (*Apis dorsata*) hives (Photo: Siddappa Shetty)*

Apis dorsata is known to be density-dependent and migrate to sites where there is a resource surge (Roubik 2005). Therefore, this leaves little scope for species other than *Palaquium* to independently attract them during this period. Post the *Palaquium* flowering period, the bees linger in the site by maintaining a low number of hives during the southwest monsoon in June-July. They abscond and arrive whenever the weather is conducive, and the hives multiply in number again in August-September – sometimes the hive density surpasses the numbers that occur during the *Palaquium* flowering period. Many secondary species such as *Elaeocarpus munronii* and *Litsea* spp., which are gregarious, come into flower along with supra-annuals during this period when the number of hives increase in the site (Figure 1). There was a distinct shift of this pattern in 2016, with a deviation from observations of 20 years.

The year 2016 was characterized by an extreme drought event that had not been recorded thus far in the site. The annual rainfall received was 1632 mm, which was nearly 200% below the annual average of 25 years. The bees arrived to the site only in September in 2016, after a delay of four months, completely skipping the *Palaquium* flowering period (as there were few individuals flowering in the year) (Figure 2). In the following year, *Apis dorsata* was completely absent during this period, as this coincided with the flowering of species at lower elevations (Devy personal observation). Therefore sequential migration of *Apis dorsata* may have evolved from tracking the phenology along the elevational range.

With predictions of more extreme events in the future, there is a likelihood that we may observe more such 'quirks' or temporary decoupling of plant-pollinators, and this could have severe implications on forest dynamics.

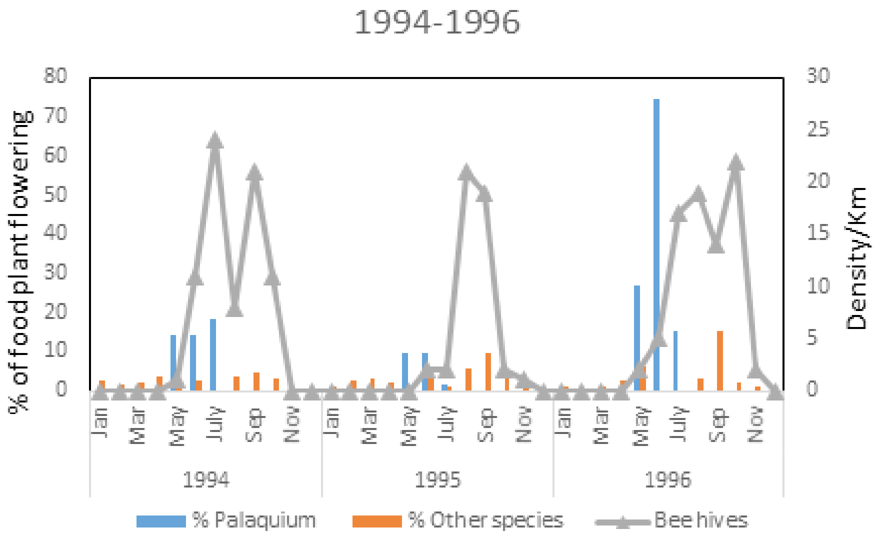

Figure 1. Bee density and food plant phenology during normal years

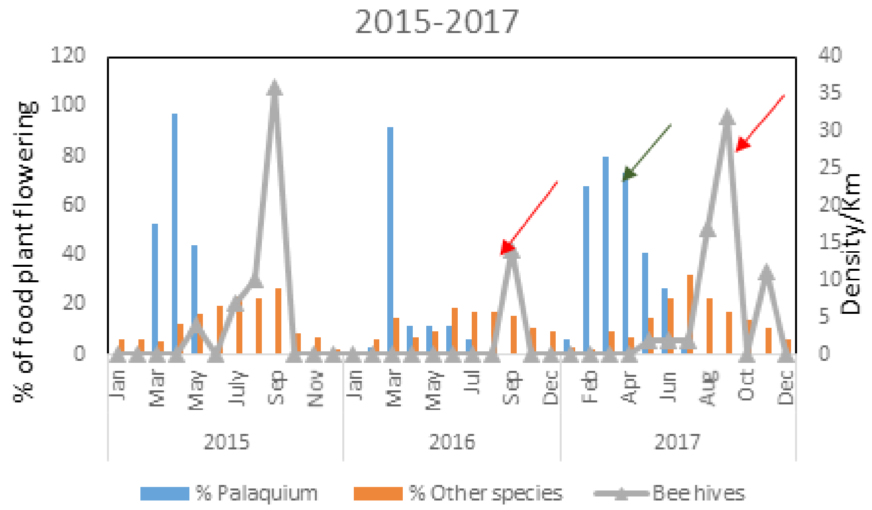

Figure 2. Bee density and food plant phenology during extreme climate years

Altitude as Proxies for Temperature Influence

The altitudinal gradient provides opportunities for powerful natural experiments to understand ecological and evolutionary responses of biota to temperature and other environmental changes (Körner 2007; Sundqvist et al. 2011; Ranjitkar et al. 2013). Mountains have therefore been regarded as an ideal natural laboratory and hence serve as proxies in climate change related research (Thuiller 2007). These studies also provide a complement to studies using long temporal time series, large spatial scales, or experimental warming/cooling manipulations (Lessard-Therrien et al. 2014). Most studies designed along the elevational gradient are reported mainly from the Andes, Rocky Mountains and the Canadian subarctic (Hoiss et al. 2012; Lessard-Therrien et al. 2014; CaraDonna and Inouye 2015). However, in recent times, there have been studies emerging from tropical mountains (Ranjitkar et al. 2013; Anderson-Teixeira et al. 2015; Du et al. 2017) A study on flowering phenology of rhododendrons along the elevational gradient of China and Nepal showed that winter temperature was the most critical variable affecting both initial flowering and peak flowering at both sites. (Hart et al. 2016; Li et al. 2016)

Apart from plants, pollinator compositions also vary along the altitudinal gradient and in general, insect pollinators are known to predominantly increase in the temperate subalpine and alpine areas (Primack 1978). A recent study on *Primula* species of the Sikkim Himalayan region showed a change in the pollinator community composition across an altitudinal gradient. Lepidopterans were the dominant visitors at lower elevations (2200-3000 m asl), bees (other than bumblebees) dominated the mid-elevations (3000-3800 m asl), and bumblebees were more dominant at higher elevations (3800-4600 m asl) (Gurung et al. 2018).

Similarly, the influence of altitude has also been noticed within specific insect taxa. For example, a study along the altitudinal gradient in the Alps (Germany), reported that the proportion of social and ground-nesting species, as well as the mean body size and altitudinal range of bee communities increased with increasing altitude, whereas the mean geographical distribution decreased (Hoiss et al. 2012). Many studies have highlighted that with warming, there could be a change in the dominance and composition of pollinator assemblage (Totland 1993; Lázaro et al. 2008), which might provide an imbalance in the species' associations with hosts. However, in the Indian context, we still require more studies designed along altitudinal gradients at the species and community level to advance our ability to predict how global warming could reshape plant-pollinator networks in fragile ecosystems, and provide valuable insights for conservation biologists.

Novel Interactions in the Face of Change

There is growing evidence that many pollinators visit plants quite opportunistically (e.g., Petanidou et al. 2008), therefore, in the absence of older pollinators, novel plant-pollinator interactions could emerge in the face of climate change (Gordo and Sanz 2005). Climate change due to warming could also mean pulses of atypical abiotic factors in certain years compared to normal years. Kremen et al. (2002) proposed a density compensation mechanism/release of certain species in agro-ecosystems under

BOX 2
Floral Traits, Phenology and Pollinators of Rhododendrons along an Elevational Gradient

Rhododendrons are recognised as keystone species in the high altitude region of the Himalaya. In Sikkim, Himalaya, rhododendrons are ideally placed across the elevation from 1800 m to more than 5000 m. This distribution pattern enables us to evaluate the influence of environmental factors on reproductive phenology and clinal variations of floral traits and frequency of pollinator visitation along the elevational gradient, and also simultaneously account for the influence of phylogenetic relationships among species.

Firstly, we assessed the influence of abiotic factors and evolutionary history on the reproductive phenology of ten co-occurring Rhododendron *species distributed across 3400 m to 4200 m in Kyongnosla Alpine Sanctuary. Our results highlight that temperature and evolutionary history are the two key drivers of early phenology events like budding and flowering, whereas later events like fruiting and fruit dehiscence are strongly associated with elevation and day length (Basnett et al., in revision).*

Further, we observed clinal variations in floral traits and pollinator taxa across species along the altitudinal gradient. Visitation rate of pollinator groups showed a strong selection for certain floral traits. Besides being able to cross-pollinate, Rhododendron *species can also self-pollinate, and representation of self-pollinated species increased along the altitudinal gradient. Birds served as an important pollinator in lower elevations, whereas bumblebees dominated higher elevations. Flies are an important pollinator group across the elevational gradient; in any given scenario when the birds and bees are scarce or absent, flies might serve as an essential secondary pollinator (Basnett et al. 2018, in preparation).*

This study suggests that species growing in increasingly limiting environments show adaptation in floral traits and flowering timing to attract certain groups of pollinators. Also, the flexibility of breeding systems and evolution of floral traits that accept multiple pollinators indicates that these systems will be able to cope with certain level of changes associated with climate change. A directional change can lead to novel interactions – more modelling with multiple parameters can throw light on this.

Flowering of R. aeruginousm *at 4200 m asl*

BOX 3
Pollinators, Climate Change and Rural Livelihoods

*Market-driven local or regional policies influence the expansion of cash crops around the globe. Cash crops introduced outside suitable ecological ranges has led to the loss of crop yield and has adversely impacted the livelihoods of small farmers. Under such circumstances, the role of soil nutrients and water requirement on crop yield has been evaluated, but pollinator requirements have seldom been investigated. We investigated the role of altitude in determining pollinator composition. Sikkim Mandarin orange (SMO henceforth) has been introduced in Sikkim Himalayas as an alternative cash crop after the failure of large cardamom due to pest attacks and the decline of its pollinator – a bumble bee species (*Bombus haemorrhoidalis*) (Sinu et al. 2011). Although the horticulture department introduced the species without considering its pollination requirements, varieties which are closely related to Sikkim Mandarin orange have been found to be pollinated by many species honeybees (*Apis spp.*) (Partap 2003).*

Farmers plucking Sikkim Mandarin orange

*Hand-pollination experiments were conducted to understand the dependency of SMO on pollinators. Pollinator visitation observations were conducted across an elevational gradient at 51 sites. Our results highlight that cross-pollinated flowers yield six times more fruit set than open/naturally pollinated flowers, highlighting the dependence of SMO on pollinators for better fruit sets. We found a gradual shift in pollinator species composition with an increase in altitude. Lower altitudes were dominated by the common honey bee (*Apis cerana*), and sites situated in higher altitudes were observed to have higher hoverfly fly abundance.*

Influence of annual mean temperature using BioClim global climate data (Pradhan et. al., in preparation) on both pollinator groups revealed honey bees to be unaffected by increased temperature, while hoverflies showed a decrease in abundance. Higher elevation farmlands which are pollinated by hoverflies are likely to be affected by warming. However, it is not clear if Apis cerana *will be able to colonize these farmlands with increasing temperatures (Pradhan et. al., in preparation). These pollinators are crucial to the success of SMO in the landscape, as more than 12000 families depend on them.*

such climatic shifts, which could be facilitated by the maintenance of pollinator diversity. Similarly, Roubik (2005) proposes that a large proportion of pollinators occupy loose niches, and that the strength of their relationship with plants can contract and expand depending on the abundance of their resource – which could be in response to the climate. He also attributes behavioural adjustments to drive pollinators' ability to adapt to changes in resource levels.

Most of tropical Asia is characterized by the occurrence of many species of honey bees which can be sympatric, a generalist flower visitor and occupy a wide range of forest types (Oldroyd et al. 1992; Devy and Davidar 2003). There was anecdotal evidence of a steep fall in the honey production in Kodagu district of Karnataka, where *Apis cerena indica* (a semi-domesticated species) succumbed to Thai sacbrood disease. Despite *Apis cerana* being one of the important pollinators of coffee, farmers did not perceive a fall in coffee production, although there was an uproar over the fall of honey flow – as *Apis dorsata*, the migratory wild honey bee appears to have compensated for *Apis cerena* (Suresh personal communication; Krishnan et al. 2012). Roubik (2005) also proposes that *Apis dorsata*, a migratory species, may compensate for and take advantage of, the local paucity of pollinators created either by mass flowering or scarcity of floral resources. India has five species of *Apis* distributed across ecosystems, and these serve as important pollinators of many crops (Otis 1996). The systems pollinated by *Apis* appear to be adapted to fluctuations, and therefore may be more resilient to changes.

Bumble bee visiting Rhododendron anthopogon
(Photo: Shweta Basnett)

NEWER APPROACHES

Molecular genetic tools have been used increasingly in the field of flowering phenology to unravel molecular mechanisms of plant response to naturally fluctuating environments in diverse plant species (Aikawa et al. 2010; Nagano et al. 2012; Satake et al. 2013; Hart et al. 2016). Some studies have integrated state-of-the-art techniques – such as 'ecological transcriptome' – wherein whole-genome transcriptome data in natural conditions, in combination with ecological and meteorological data, is analysed to understand the processes of how plants respond to dynamic and complex environments (including pollinator interaction) (Kobayashi and Shimizu 2013). Transcriptome studies are mostly restricted to a very few temperate regions (Shimizu et al. 2011).

In the past 4-5 years, the integration of genetic studies with phenological observations has emerged. Plant species interact with their population, community, pollinators and herbivores, and have prolonged exposure to temperature at the regional scale as well as local climate. Natural habitats are characterized by large, stochastic fluctuations which often do not reflect in molecular genetic studies under laboratory conditions, and therefore, may not be adequate to study responses to changing environments (Shimizu et al. 2011). There is an urgent need to combine molecular biology with long-term ecological and meteorological data, to aid construction of predictive models on population genetics in natural conditions. Species responsiveness to year-to-year climate variation can be linked to their long-term persistence versus extinctions. A molecular approach will also help us understand if certain traits might favour species to be more resilient in a system. For example, in Mt. Yulong, the last flowering *Rhododendron* species were phylogenetically clustered and adapted to reduced fruit size and fruit development time, which may have reflected the reduced time available to complete their reproductive cycle and also interact with their pollinators before the harsh winter (Hart et al. 2016).

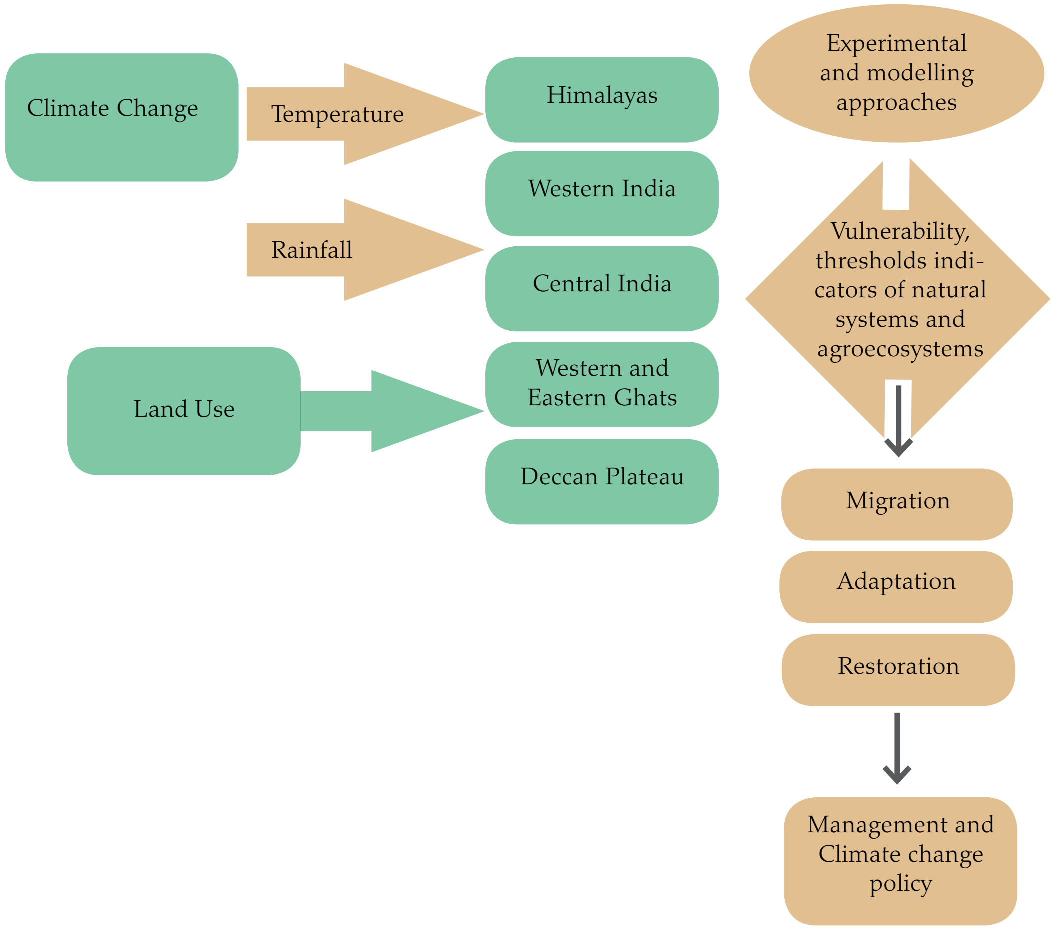

Figure 3. Adapting and mitigating strategy of pollinators and pollination systems

Response to the variations of climate can also come in the form of gradients in flower output and sexual expression (male-to-female ratios in dioecious and monoecious species), which can influence pollen flow and fruit-set through pollinators and have implications on genetic diversity. Besides the response of pollinator taxa, these variations might also have an imprint on genetic composition which might determine the recruitment success of the species. However, most studies still lack information on pollinators which are closely associated with flowering timing (Lázaro et al. 2013). It is becoming essential to study the shared influence of abiotic factors, pollinators, and evolutionary history – all of which interactively shape flowering events (Cortés-Flores et al. 2017).

Pollinators not only support biodiversity and genetic diversity, they also contribute to the high productivity in 35% of crops grown around the world, thereby substantially increasing global food security (Klein et al.2007). The population of the world is predicted to escalate to 9-10 billion by 2050, and demand for food could increase many fold (Ellis et al. 2015). The negative impacts of climate change and the pollinator crisis would threaten food security drastically (van der Sluijs and Vaage 2016). Also, the reliance on managed pollinators is increasing to meet the demand for pollinator-dependent crops, the growth of which is being expanded (Aizen and Harder 2009). There is global consensus that besides climate change, multiple stressors such land use and land cover change, pollution and changing food habits can lead to pollinator decline globally and at regional levels (Potts et al. 2010).

This complexity coupled with multiple causative factors can contribute to pollinator decline of both wild and cultivated species, and this demands adequate monitoring systems. Through Indian case studies set in the larger context, we have highlighted that a warming climate and changing precipitation regimes are likely to have variable responses from plant-pollinator systems. While isolated efforts are just emerging, there is an urgent need to monitor pollinators and their interactions through coordinated efforts in natural and agricultural systems at the scale of the country (Mayfield and Belavadi 2008; Krishnan et al. 2012; Carr and Davidar 2015; Bhattacharya and Basu 2018 and also see Box 1, Box 2 and Box 3).

Firetailed sunbird one of the active pollinator of Rhododendron thomsonii *(Photo: Shweta Basnett)*

Coordinated experiments across a network of field sites that represent major ecosystems and agro-ecosystems, with integration of meteorological data, will help in identifying vulnerability, thresholds and indicators of climate change effects on plant-pollinator interactions. Also, climate change response is likely to vary across regions and within ecosystems. Natural ecosystems and agro-ecosystems covering the entire geography of the country should be represented in order to capture the variability in response in terms of vulnerability and thresholds, and also identify indicators. This could feed into management at a local scale as well as the level of national policy (Figure 3).

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Butterflies in a Changing Climate

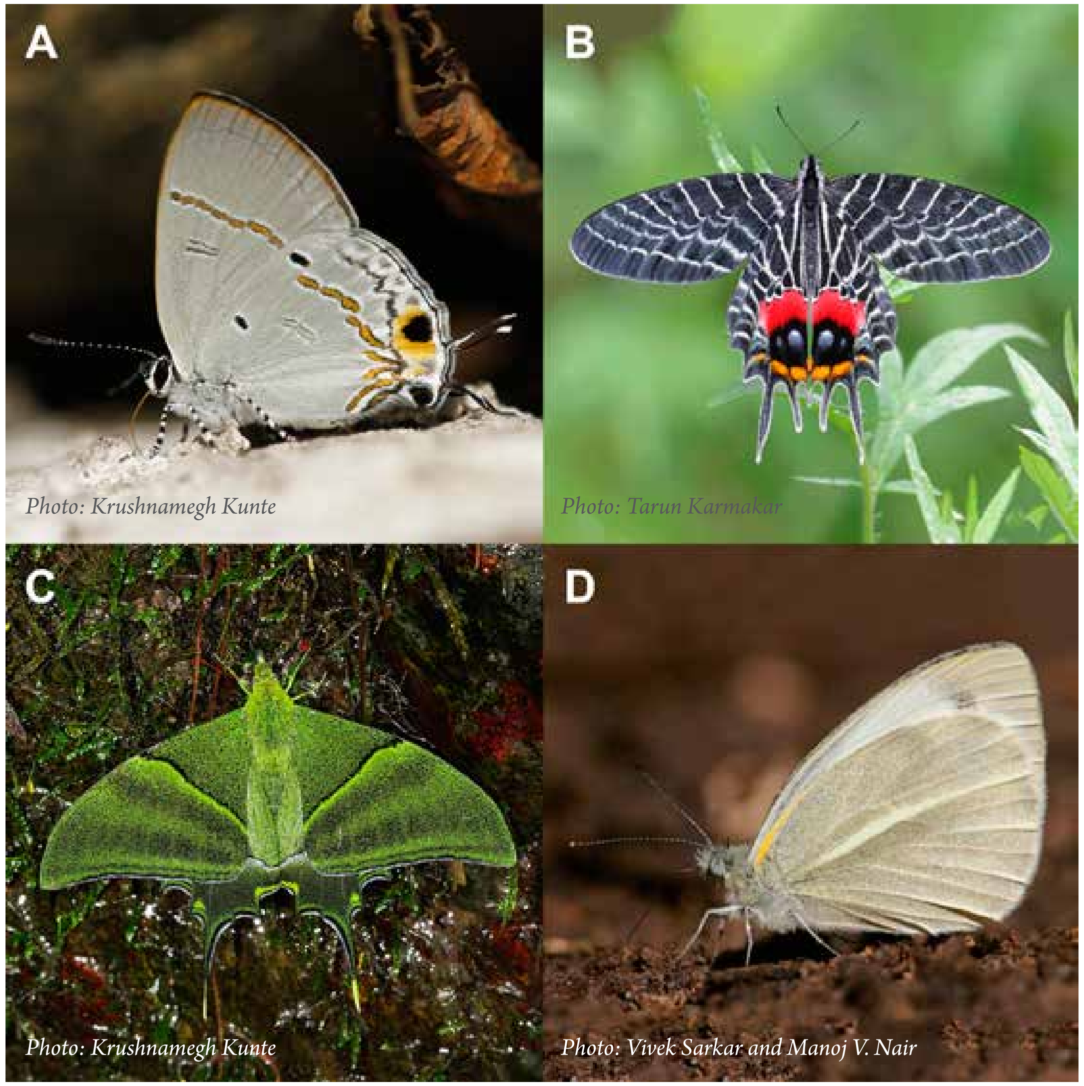
Krushnamegh Kunte

Photo: Krushnamegh Kunte

Changing climate and associated ecological factors have contributed to great episodes of species diversification in the history of life on Earth. These factors have led to such spectacular species radiations as flowering plants and butterflies, through cycles of glacial and interglacial periods (Peña and Wahlberg 2008). And yet, plants and animals are largely failing to cope with the pace at which human activities are altering and destroying habitats and fuelling long-term changes in climatic conditions. For cold-blooded insects such as butterflies, vulnerability to climate change stems from shifting, contracting ranges and local extinctions (Chen et al. 2011; Devictor et al. 2012), and species-specific traits related to host plant use and diet breadth, early-stage diapause, and range sizes (Diamond et al. 2011; Radchuk et al. 2013). These are complex biological problems that are tightly linked to the survival of a large number of species.

Two of the most prominent negative impacts of climate change on butterflies are: (1) poleward and upward shifts in distributional ranges of butterflies, which reduce available habitat for the species and cause local population extinctions (Chen et al. 2011; Devictor et al. 2012), and (2) changes in breeding phenology, i.e., the timing of egg-laying, pupal diapause, emergence of adult butterflies, etc., and their impacts on survival of different life stages and reproduction (Diamond et al. 2011; Radchuk et al. 2013). They may also deprive butterflies of critical larval host plants even though other climatic conditions may be suitable (Parmesan 2006; Radchuk et al. 2013). Thus, impacts of climate change on butterflies manifest through several ecological interactions and other biological factors.

Butterfly populations are particularly vulnerable to effects of climate change across India's biodiversity hotspots. These hotspots contain prominent altitudinal gradients (Himalaya, NE India, and Western Ghats) and oceanic islands (Andaman and Nicobar Islands) that host high levels of species diversity and endemism. Plant and animal communities associated with these ecological conditions are particularly vulnerable to climate-driven disruptions in species interactions, and eventual population extinctions (Parmesan 2006). However, there is little work on the impacts of climate change on the biology and conservation of Indian butterflies. It is critical that such studies are urgently integrated into national biodiversity and climate change programmes as implemented by various scientific research and conservation agencies of the Government of India, and non-governmental agencies.



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Indian butterflies are vulnerable to impacts of climate change. Changing rainfall patterns and temperature regimes in the Himalaya and NE India likely affect distributional ranges, activity periods and breeding biology of butterflies. A: The banded tit (Hypolycaena narada) *has a single, short flight period of less than three weeks. B: The Bhutan glory* (Bhutanitis lidderdalii) *has specific host plant associations, and its reproductive bouts are heavily dependent on specific climatic envelopes. C: Kaiser-i-Hind* (Teinopalpus imperialis) *is a mid-elevation specialist and, like the Bhutan glory, a legally protected species in India. D: Asian cabbage white* (Pieris canidia) *is commonly seen around agricultural fields in the Himalaya. Darkening of its wings during pupal development is a key thermal adaptation for seasonally fluctuating and altitudinally changing climatic conditions.*

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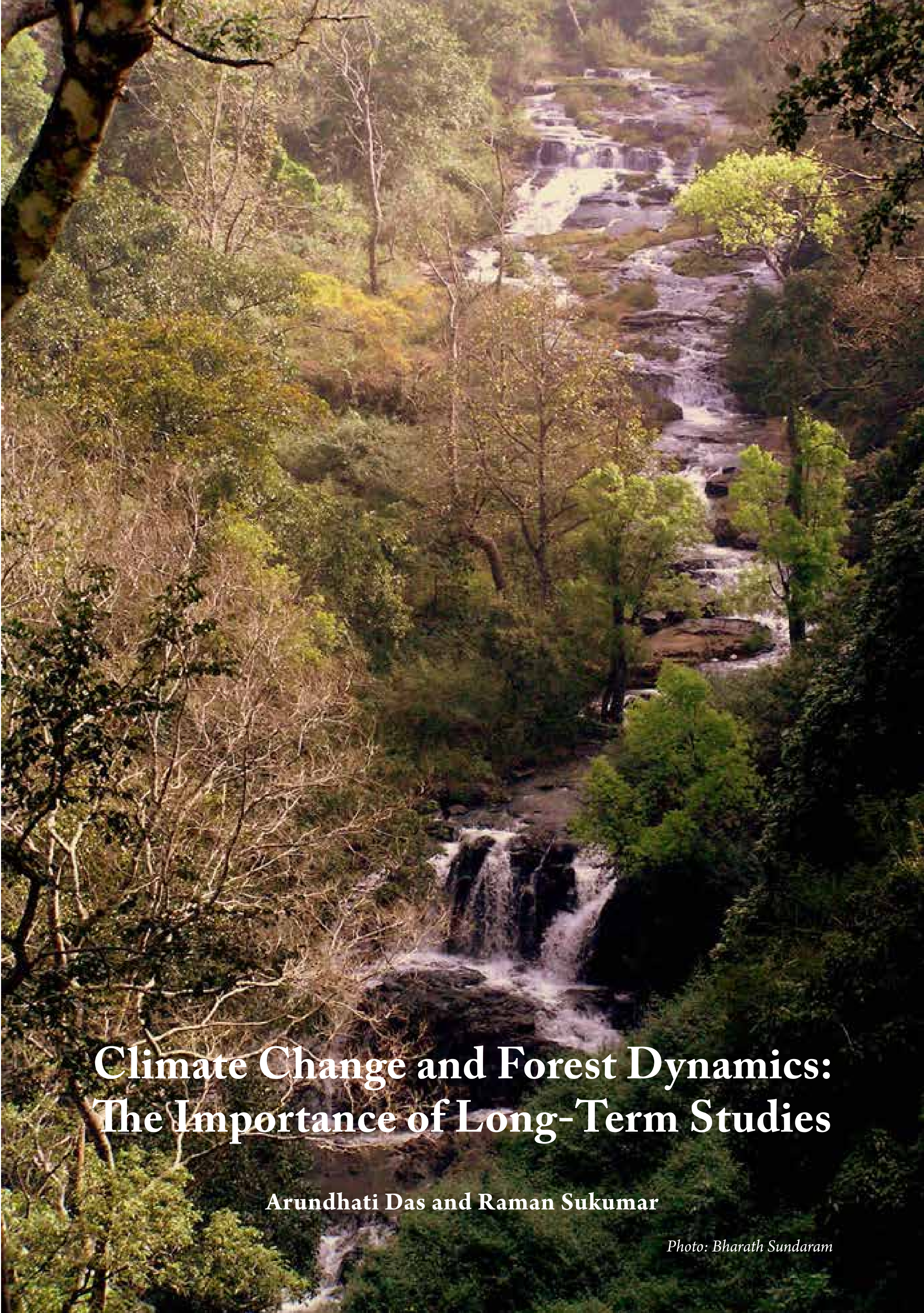

Climate Change and Forest Dynamics: The Importance of Long-Term Studies

Arundhati Das and Raman Sukumar

Photo: Bharath Sundaram

INTRODUCTION

Forests are repositories of much of the biodiversity and carbon stocks globally. In the context of ongoing and future climate change, driven largely by anthropogenic greenhouse gas (GHG) emissions, the role of forests in carbon fluxes will be important in possibly mitigating the rise of the most important GHG, carbon dioxide, in the atmosphere (Pan et al. 2011). Globally, it is estimated that forests hold 860 ± 70PgC (Pan et al. 2011). Of the carbon stocks held in forests, 54.6% is held in tropical forests, 31.6% in boreal forests and 13.8% in temperate forests. The carbon stored in tropical forests is greater in biomass (56%), while in boreal forests it is higher in the soil (60%) (Pan et al. 2011).

Between 2000 and 2007, undisturbed and regenerating forests sequestered 4.0 ± 0.7 PgC yr^{-1} (Pan et al. 2011). Deforestation and land use and land cover change (LULCC), mainly in the tropics, led to losses of forest carbon stocks estimated at 2.8 ± 0.4 PgC yr^{-1}. Hence forests represent a net global carbon sink of 1.1 ± 0.8 PgC yr^{-1} (Pan et al. 2011; Settele et al. 2014), but there are several uncertainties in these estimates (see Cox et al. (2013), Joseph Wright (2013), Tian et al. 2016). Global studies also show that the terrestrial carbon sink may have increased in the last few decades (Ballantyne et al. 2012), with an estimated average increase of 0.34±0.11 Mg C $ha^{-1}yr^{-1}$ in standing forest biomass (Anderson-Teixeira et al. 2015). This indicates a possible fertilization effect of increasing CO_2 and temperature on plant growth, as well as the role of other factors such as nitrogen deposition, increased plant water-use efficiency and recovery from disturbance (Keenan et al. 2013; Settele et al. 2014), however, there are several uncertainties here too (Friend et al. 2014).

Modelling studies indicate that rising temperatures, ozone concentrations, droughts and fires will lead to further weakening of the forest carbon sink, and even a possible transition to forests being a net carbon source by the end of the century (Settele et al. 2014). Increased tree mortality and forest loss due to effects of climate change, particularly increased frequency of drought, fire and pathogen outbreak, has been observed over the last few decades (Allen et al. 2010). Experimental and modelling studies show that photosynthesis and water use efficiency continue to increase in many forests, but at a progressively slower rate, up to approximately 600 ppm CO_2. There is strong evidence that decreasing availability of nitrogen and other nutrients will further limit the ability of plants to respond to increasing CO_2 (Settele et al. 2014).

Indian forests cover 7,08,273 km^2 (21.54% of the country) and vary greatly in their species composition, canopy closure, stand structure, topographic complexity, seasonality and disturbance regimes (Forest Survey of India 2017). This spectrum includes mangroves, tropical moist and dry deciduous forests, savanna-woodlands, subtropical and temperate forest (Figure 1). Much of this variation is driven by spatial variation in temperature and rainfall (Champion and Seth 1968). In order to understand how changes in climatic variables could affect forest dynamics and – ultimately carbon storage across various forest habitats – we need studies across all major forest types that can scale up in space from the community to the landscape, regional and subcontinental scales. Such studies would systematically incorporate spatial variation in structure and dynamics of forest types at the landscape and regional scales in response to environmental gradients, as established in the Amazon (Lewis et al. 2004).

It is also important to study forest dynamics in the long term (at least decadal) for several reasons. The underlying processes of tree community dynamics such as regeneration, stem growth and mortality vary enormously from one year to another in response to prevailing ecological and environmental factors. Indeed, environmental stochasticity is the most important driver of forest dynamics not only in highly seasonal tropical dry forests (Sukumar et al. 1998, Sukumar et al. 2005), but across a spectrum of tropical forests including rainforests (Chisholm et al. 2014). Unless decadal scale variability in the processes of forest dynamics is understood, it is unlikely that changes in diversity or carbon stocks in response to climate variability and change would be adequately represented.

LONG-TERM STUDIES

A Brief Account of Long-Term Studies Globally

The Center for Tropical Forest Science (CTFS) – Forest Global Earth Observatory (ForestGEO) (https://forestgeo.si.edu) is a global (25°S–61°N) network of research sites, established in the 1980s to study long-term forest dynamics using large-sized plots. It now consists of 59 long-term sites in 24 countries, all of which are being monitored continuously, some since as early on as 1981 (Anderson-Teixeira et al. 2015). The network is designed to facilitate cross-site comparisons by applying a standardized tree census protocol across all major forest biomes. Mangrove, swamp and peat forests are however not represented. Plot sizes range from 2-120 ha (median 25 ha). Within each plot, all free-standing woody stems ≥1 cm dbh are censused once every 4-5 years. Fine-scale topography is mapped for studying habitat associations. Other measurements on several aspects of forest ecology, including trophic interactions, are also made using standardized frameworks (Anderson-Teixeira et al. 2015). In total, the network currently monitors 1653 ha of forest containing over 5.7 million stems, representing more than 10,000 species. Most sites tend to be in relatively undisturbed old-growth or secondary forest areas that are subject to a range of natural disturbances. However, human influence through global change factors is pervasive across all sites (Anderson-Teixeira et al. 2015).

The Amazon Forest Inventory Network (RAINFOR; http://www.rainfor.org/) was established in 2000 as an international collaboration between scientists studying forest dynamics in the Amazon. The network monitors long-term trends in forest biomass in relation to soil and climate across more than 50 long-term study sites in the Amazon, and also aims to understand the future impacts of global change on forest dynamics at multiple spatial scales, as well as the basin-wide carbon balance in the Amazon. It also focuses on understanding patterns of biodiversity in relation to climate and soils. A similar network has been established for long-term studies on tropical rainforest dynamics in Africa (African Tropical Rainforest Observation Network or AfriTRON; http://www.afritron.org/), to understand the biogeochemistry and links between biodiversity and ecosystem function in those forests.

Long-Term Studies in India

Long-term studies in Indian forests have been undertaken since the early 1900s, mainly by National and State forest research institutions and more recently by academic institutions (Tewari et al. 2014). The earliest plots were established to study tree growth (basal area and diameter increment) and mortality, especially for timber species such as *Hopea parviflora* and *Shorea robusta* in natural forests (Tewari et al. 2014). These plots were established in Karnataka and

Uttar Pradesh by the Forest Research Institute (FRI) and State Forest Departments.

The network of plots in natural forests was greatly expanded during the 1930s and beyond, to include linear tree increment plots (LTIs; n = 48, 20m width by variable length, area range: 1.09-14.72 ha), linear increment plots (LIPs; n = 35, area range: 2-8.55 ha), linear sample plots (LSPs; n = 7, area range: 1.2-4 ha) and permanent preservation plots (PPPs; n = 187, area range: 0.01-4000 ha). These plots were established between 1924 and 1985 and monitored at five-year intervals, most till 1994.

The rainforests and deciduous forests of the Western Ghats are relatively well represented within this network, as are the deciduous forests of Uttar Pradesh and Bihar (Figure 1). LTIs in rainforests of Karnataka and Tamil Nadu were monitored for about 50 and 57 years respectively, till 1994. A few LTIs were established between 1931 and 1985 in the dry deciduous forests of Maharashtra and monitored every 10 years. Finally, LTIs in *Shorea robusta* forests of Bihar were established between 1936 and 1968 and monitored till 1981 (Tewari et al. 2014). Three LIPs were established in rainforests of Assam between 1958 and 1978, and the rest were in the dry deciduous forest of Uttar Pradesh. The latter were monitored for about 51 years, till 1990. LSPs were established in the dry and wet mixed forests of Assam and West Bengal in the 1920s and monitored till 1994 (Tewari et al. 2014).

Most of the PPPs were established in northern moist and dry deciduous forests. The earliest plots were established in 1905, in *Shorea robusta* forest in Bihar. Unfortunately, much of the data from PPPs is not accessible in the current scientific literature (Tewari et al. 2014). In 1988, a 50 ha long-term forest dynamics plot was established in the tropical dry deciduous teak forests of Mudumalai Wildlife Sanctuary (Sukumar et a. 1992). The Mudumalai Forest Dynamics Plot (MFDP) is part of the CTFS-ForestGEO network and follows standardized protocols for measuring forest dynamics (Anderson-Teixeira et al. 2015). The plot has been censused every year, with all stems re-measured every four years, for the last 30 years. The MFDP is the longest running monitoring effort encompassing all aspects of forest ecosystem ecology in India, and one of the few plots within the CTFS-ForestGEO network representing the dynamics of tropical dry deciduous forests. Therefore, from both the national and global perspectives, the MFDP provides a unique window on long-term forest dynamics.

The research at the MFDP was supplemented during the early 1990s by a series of 19 one-hectare plots across the steep rainfall gradient at Mudumalai to better understand the role of moisture in forest dynamics (Dattaraja et al. 2018). More recently, a Permanent Sample Plot was established in rainforests at Uppangala in the Karnataka Western Ghats (UPSP), and is being monitored by the French Institute of Pondicherry and the Karnataka State Forest Department. There is now considerable insight into the growth and dynamics of this dipterocarp-dominated low elevation rainforest, built on more than 18 years of research and monitoring (Pascal and Pelissier 1996).

Other long-term forest monitoring efforts (with >20 years of data) have been undertaken in Kalakkad Mundanthurai Tiger Reserve and in Biligiri Rangaswamy Temple Tiger Reserve in Karnataka by scientists at Ashoka Trust for Research in Ecology and the Environment (Hiremath et al. 2017). A collaborative effort to establish 1 ha long-term forest monitoring plots across an environmental gradient of forest types was recently initiated by scientists at the National Centre for Biological Sciences; this is currently underway at seven sites across the country (https://lemonindia.weebly.com/).

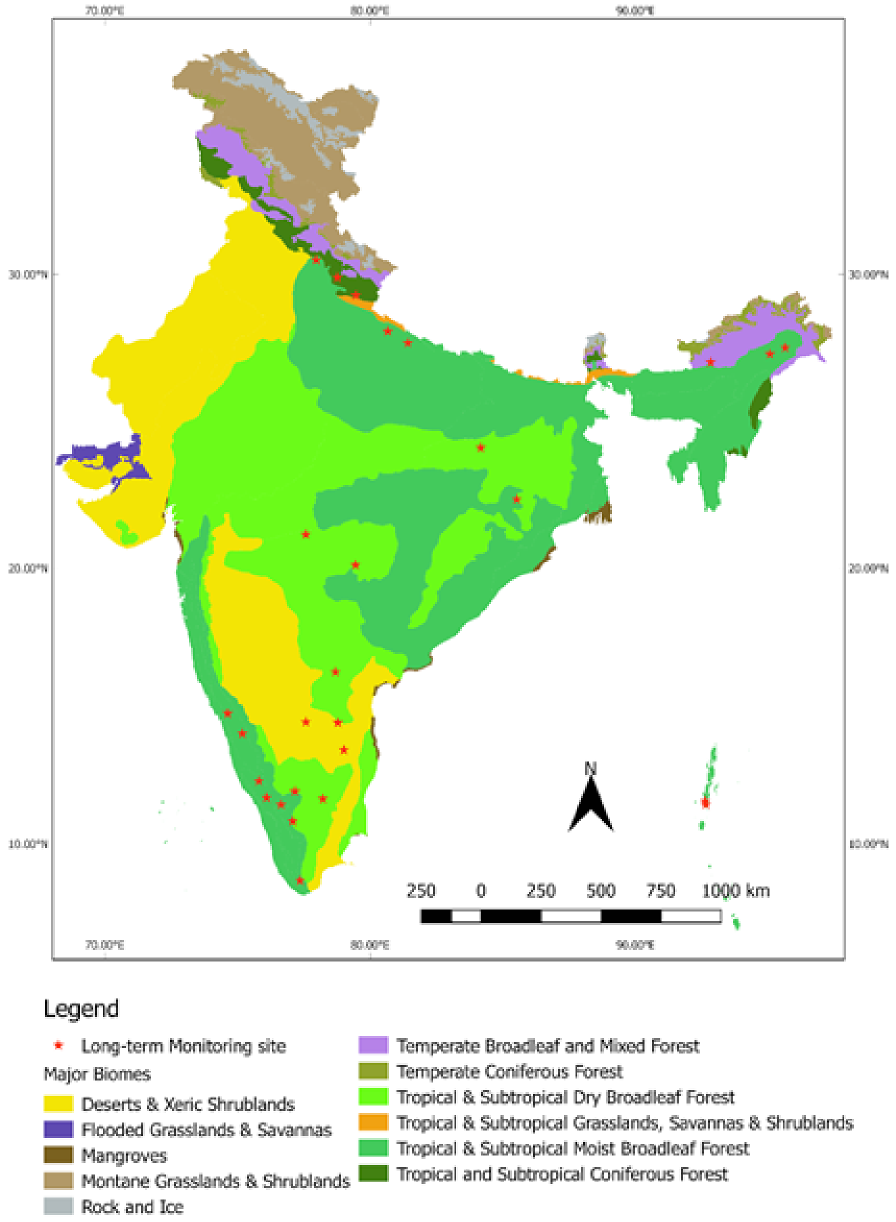

Figure 1. Map of long-term forest monitoring sites (locations from Tewari et al. 2014, Hiremath et al. 2017 and https://lemonindia.weebly.com/) superimposed on major biome types (Olson et al. 2001). Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

The majority of long-term forest studies are located in the Western Ghats of India, a biodiversity hotspot. The forests of western and eastern Himalaya and other parts of north-east India, as well as central India remain poorly represented in the existing network of long-term forest study sites (Figure 1).

The following section summarises key findings on different aspects of forest dynamics, much of which has been gained through sustained research efforts at the MFDP and UPSP.

Strobilanthes spp. blooming in shola, Mukuthi National Park (Photo: Arundhati Das)

KEY RESULTS FROM LONG-TERM STUDIES IN INDIA

Tree Demography in Tropical Dry Deciduous Forests

Tree recruitment and mortality rates in tropical dry deciduous forests (TDDFs) vary greatly over time (Sukumar et al. 2005). Data from the MFDP indicate that from an initial population of 26,000 (belonging to 72 woody plant species >1 cm dbh) in 1988, the number of individuals declined steeply (–57%) over the next eight years, followed by an almost 2.5-fold increase over the ensuing 12 years to amount to 37,000 individuals representing 80 species (Tewari et al. 2004).

Overall recruitment rate (new stems >1 cm dbh) averaged 4.4% over the first 12 years of monitoring in the MFDP (Sukumar et al. 2005). Recruitment rates varied greatly with the occurrence of dry season fires (2.2-6.0% annually). In one particular year without fire (1999-2000) recruitment peaked at 12.6%. Most of the large increases in recruitment between 1996 and2008 were due to the vegetative recruitment of three understorey species (Tewari et al. 2014). *Cassia fistula*, in particular, accounted for 50% of all recruits between 1988 and 2000 (Sukumar et al. 2005).

Ramaswami and Sukumar (2013a) found that dominant canopy species like *Lagerstroemia microcarpa* and *Terminalia crenulata* were not represented in the seedling size class. No recruitment was observed for *Anogeissus latifolia* and *T. crenulata* between 1988 and 1996 (John and Sukumar 2004), and very few stems have been recruited since then. In general, recruitment rates were low for canopy species, with the exception of *L. microcarpa* and *Tectona grandis*. These species also showed negative density dependence and distance effects on recruitment, indicating potential influence of pests and pathogens or other factors on recruitment (John and Sukumar 2004). Recruitment of new stems is almost exclusively (>99%) by vegetative means through coppicing or sprouting from roots or rhizomes (Sukumar et al. 2005). Not much information is available regarding recruitment at the seedling stage and transitions from seedling to sapling stage. However, Ramaswami and Sukumar (2013a) found that the probability of seedling survival increased with increasing annual rainfall.

The average annual mortality rate (1988-2007) across all stems >1 cm dbh was 6.9 ± 4.6% (range 1.5-17.5%) (Suresh et al. 2010). In general, smaller stems (1-5cm dbh) had higher rates of mortality (22.2 ± 17.4%) compared to medium (5-10 cm dbh; mortality 4%) and large (>30cm dbh; mortality 0.6%) stems (Suresh et al. 2010, Sukumar et al. 2005). Mortality of large trees in the MFDP (>30cm dbh) was found to be quite low when compared with data from other moist tropical forest and rainforests globally (Condit et al. 1999). Antin et al. (2016) report a mortality rate of 0.88% per year, across all species, from a 17-year study of dynamics in a 5 ha permanent sample plot in a Western Ghats rainforest. In the MFDP, yearly variation in mortality by size class was highest in smaller stems, followed by medium stems, depending on the incidence of disturbance factors such as fire and elephant herbivory (Suresh et al. 2010, Sukumar et al 2005). Data from evergreen forests also indicate a similar pattern of decreasing probability of mortality with increasing diameter for smaller trees (up to 30 cm dbh) (Elouard et al. 1997).

The primary causes of mortality in tropical dry deciduous forests include fire, elephant herbivory, and to a lesser extent, drought (Sukumar et al. 2005; Suresh et al. 2010; Chitra-Tarak et al. 2018). In the MFDP, the average fire-return interval was estimated to be 1.7-2.9 years (Mondal and Sukumar 2016). More than 80% of the plot was burned in 6 out of 22 years (Pulla et al. 2016). Smaller stems were the most vulnerable to fire (Sukumar et al. 2005). Elephant-related mortality was highest in medium sized stems (5-10cm dbh), particularly for plants of the order Malvales (Suresh et al. 2010). Between 1988 and 1991, elephant herbivory was largely responsible for a 66% decline in the population of *Kydia calycina* (John and Sukumar 2004). In low fire years, mortality of medium stems was similar to or greater than that of smaller stems, due to elephant damage (Sukumar et al. 2005).

Variability in rainfall has been shown to be correlated with mortality, either directly through droughts that have a decadal return time, or indirectly, on shorter timescales, through increasing vulnerability to fire or other natural causes (Suresh et al. 2010). Mortality of 1-10 cm dbh stems was negatively correlated to rainfall in the previous year, while that of larger stems was negatively related to rainfall with a 3-year time lag (Suresh et al 2010). In 2004, mortality peaked following a 3-year drought (Chitra-Tarak et al. 2018). Prolonged drought was found to selectively increase mortality of deeper-rooted species, as these tend to access water from deeper parts of the vadose zone (up to 35 m below ground), which once depleted, take longer to recharge. Hence, vulnerability to prolonged droughts depends on species-specific traits of hydraulic uptake and below-ground availability of water (Chitra-Tarak et al. 2018).

Other causes of mortality included diseases, pests and wind damage. Sukumar et al. (1992) report probable widespread mortality of mature individuals of *Shorea roxburghii*, possibly caused by the spread of a stem-borer (cerambycid) beetle.

Patterns of Growth

The growth of tropical trees is influenced by a number of species-specific traits (e.g. life history, adult stature and wood density), ontogeny as well as environmental factors such as climate, topography, availability of light or water, and strength of competition (Nath et al. 2006; Le Bec et al. 2015; Antin et al. 2016; Chitra-Tarak et al. 2018).

In tropical evergreen forests, where access to light is limiting, canopy species could allocate more resources to rapid height growth, in order to reach the canopy faster (Poorter et al. 2005), whereas understorey species could allocate more resources to increase crown width, in order to intercept more of the light that filters through (Antin et al. 2016). In low elevation dipterocarp forests in the Western Ghats, the four most dominant species (representing >48% of stems and 55% of the basal area; Elouard et al. 1997) have distinct growth and reproductive strategies, corresponding to their relative positions in different forest layers. For instance, *Dipterocarpus indicus* dominates the emergent layer, while *Vateria indica*, an upper-canopy species – well represented across all size classes – shows rapid growth response to its light environment. *Myristica dactyloides*, a lower canopy species, shows limited growth in height and girth and only forms the canopy in the absence of upper canopy and emergent species. Finally, *Humboldtia brunonis* dominates the understorey and flowers and fruits year-round (Elouard et al. 1997; Antin et al. 2016).

Apart from species-specific and ontogenetic differences in growth strategy, allocation of resources to increase in height as opposed to girth is further influenced by environmental factors such as climate, topography, and competitive neighbourhood (Le Bec et al. 2015; Antin et al. 2016). These factors contribute to the tremendous variability in growth, even within a species (Le Bec et al. 2015). Pélissier and Pascal (2000) found that while seasonal diameter variations were positively correlated with rainfall and soil moisture, average annual growth was higher in the drier year of the two-year study.

Stand density and basal area vary with topography (i.e. slope and aspect), which strongly controls soil moisture and access to light. Trees on gentle slopes tend to increase in height faster compared to those on steep slopes, where there is greater access to light (Le Bec et al. 2015; Antin et al. 2016). *V. indica* grows faster earlier on east-facing slopes, compared to west-facing ones. Over an 18-year period, basal area increment for *V. indica* was greatest on gentle, east-facing slopes (35.4%) and, while it was greatest for *D. indicus* on steep, east-facing slopes (17.1%) (where its primary competitor, *V. indica*, is less dense and had the least increment in basal area (12.7%)).

In general, *V. indica* grew faster than *D. indicus*, almost doubling its basal area over the study period. However, growth of smaller individuals of *V. indica* decreased more with increasing competition, compared to *D. indicus* (Antin et al. 2016). Due to low disturbance rates in these forests, the competitive neighbourhood of an individual and its effects on growth rate is unlikely to change over decadal time-scales (Le Bec et al. 2015). Inter-annual variability in climate was not found to be a strong driver of tree growth compared to other factors (Le Bec et al. 2015).

Between 1993 and 2011, stand basal area of the permanent sample plot at Uppangala increased by more than 7.8%, from an initial value of 41.8 m^2/ha. An even greater increase (11.2%) was recorded on gentle east-facing slopes. The initial stand density was 650 trees ha^{-1} and remained almost constant over the study period (–0.02% change in trees/ha/yr) (Antin et al. 2016).

In comparison, data from the tropical dry deciduous forest of the MFDP also indicate a 5.7% increase in basal area from 24.4 m^2/ha to 25.8 m^2/ha, between 1988 and 2008. However, the greater environmental stochasticity in these forests caused much higher fluctuation in stand density over time: decreasing from 520 stems ha^{-1} in 1988 to 300 stems ha^{-1} in 1996, and then increasing to 740 stems ha^{-1} by 2008 (Suresh et al. 2011). Most of this fluctuation is driven by stems under 30 cm dbh, while the larger stems actually show increases over time (Sukumar et al. 2005).

As in evergreen forests, growth patterns tend to vary greatly both by size class of stems, as well as by species (Nath et al. 2006). The average growth rates of all stems during three consecutive census intervals (between 1988 and 2000) were 3.32 ± 3.36 mm/yr, 1.84 ± 3.03 mm/yr and 2.71 ± 3.11 mm/yr respectively. The reduction in growth rates in the second interval was associated with a large decrease in annual rainfall. Therefore, regardless of species or size class, stem growth in this forest appears to be more sensitive to variation in large-scale climatic factors (Nath et al. 2006). The smallest stems were found to grow the fastest. In fact, average growth rate of the smallest trees were higher than those reported from other tropical forests globally (Nath et al. 2006). Unlike in rainforests, tree size did not affect rate of growth much, and no consistent differences in growth rate were found between canopy and understorey species. The latter reinforces the notion that light availability does not strongly determine variation in growth in these forests, given their relatively open canopy (Nath et al. 2006). Woody productivity and total basal area

Enumeration of the 50ha plot in Mudumalai (Photo: R.Sukumar) were found to increase with mean annual precipitation and nutrient availability across a series of 1 ha plots that span a mean annual rainfall gradient of 600-1800 mm in the Mudumalai forests (Dattaraja et al. 2018).

Despite high intraspecific variation, species identity was able to account for 16% of the overall variation in growth rates between 1988 and 2000. Four dominant canopy species, *L. microcarpa*, *T. crenulata*, *A. latifolia*, and *T. grandis*, comprised 43% of all individuals in 1988 (Sukumar et al. 1992). *T. crenulata* and *A. latifolia* appeared to have relatively slower growth compared to the others, especially at the juvenile stage (Nath et al. 2006).

Recent eco-hydrological studies show that these species differ greatly in the mean depths at which they access below ground water resources in the vadose zone (Chitra-Tarak et al. 2018). *T. crenulata* tends to access water in the deepest compartments, followed by *A. latifolia*, while *L. microcarpa* accesses water mainly from intermediate depths and *T. grandis* from relatively shallow depths. Species' hydraulic uptake traits and below-ground water availability were better able to explain interspecific growth variation, especially during periods of water stress, compared to cumulative rainfall in the inter-census interval (Chitra-Tarak et al. 2018). Therefore, while niches of dominant species in rainforests seem to be partitioned along a light gradient, in dry deciduous forests, this partitioning occurs along a gradient of below-ground water availability (Chitra-Tarak et al. 2018).

The fact that almost all regeneration in TDDF is vegetative leads to a temporal disconnect between above- and below-ground growth in these forests, allowing growth of above-ground components to fluctuate more and generally to show greater plasticity (Nath et al. 2006) in the face of frequent disturbance and environmental stochasticity on short timescales. This may be why stem size is not a good predictor of growth, unlike in more aseasonal forests (Nath et al. 2006). It could also explain why smaller stems have comparatively greater capacity for fast growth compared to those in other tropical forests, as they are connected to below-ground structures that have persisted for longer and are therefore likely to be more established and better able to harvest resources.

The Role of Fire

Fire, originating from both natural and anthropogenic sources, is a major driver of dynamics at sub-decadal time scales in Indian forests (Kodandapani et al. 2008). Fire extent, frequency and intensity are determined by the interplay of climatic factors and standing vegetation. The former determines the level of moisture in forest fuel load, while the latter determines the quantity and quality of fuel (Mondal and Sukumar 2016). Hence, over time, the number of fire detections annually between 2003 and 2016 showed peaks corresponding to drought years in 2004, 2009, 2012 and 2016 (Forest Survey of India 2017). Studies from TDDF find that fire-induced tree mortality is significantly negatively related to amount of rainfall in the previous year (Suresh et al. 2010). Wetter forests may burn more extensively following periods of prolonged or intense drought (Mondal and Sukumar 2016). During the drought years of 2012 and 2016, the proportion of fires in moderately dense and very dense forests were higher than that of open forests, indicating that vulnerability of these forest types to fire over time is strongly modulated by drought (Forest Survey of India 2017). In terms of spatial pattern, there is a unimodal relationship between fire occurrence and average annual rainfall. Regions with intermediate annual rainfall tend to have greater incidence of fire compared to those at either extreme of the gradient (Mondal and Sukumar 2016). Fires in wet forest types, especially tropical rainforests, tend to be limited by fuel moisture content, while those in arid forest types (e.g. dry thorn scrub), tend to be limited by availability and patchiness of fuel (Mondal and Sukumar 2016).

Forestfire in BRT (Photo: Bharath Sundaram)

Seasonally dry forests are affected by both variation in fuel load as well as fuel moisture content. In these forests, seasonality of rainfall also influences the occurrence and extent of burning. Wet season rainfall is related to forest productivity, which in turn determines dry season fuel load. Rainfall amount and timing during the dry season determines the moisture content in forest fuels (Mondal and Sukumar 2016). In wetter (but still seasonally dry) forest types, the proportion of area burned decreases with increasing levels and duration of dry season rainfall. In the drier forest types, the extent of burning was highest when dry season rainfall was low and wet season rainfall in the previous year was high, and also in years with low wet season rainfall and high early dry season rainfall. In dry thorn scrub forests, the amount of area burned was most significantly related to levels of wet season rainfall, as these forests are more fuel-limited (Mondal and Sukumar 2016).

The number of forest fires in India, between 2003 and 2016, were highest in tropical moist forests, TDDFs and tropical semi-evergreen forests, and lowest in tropical and subtropical dry evergreen, alpine scrub and Himalayan dry temperate forests (Forest Survey of India 2017). Average Fire Radiant Power (FRP), a measure of energy released through fire –corresponding to the amount of fuel burned – was highest in subtropical broadleaved hill forests (83 MW), followed by montane wet temperate forests (76.7 MW), tropical semi-evergreen (76.6 MW) and tropical moist deciduous forests (50 MW). TDDFs had the lowest average FRP values (23 MW), indicating lower intensity fires (Forest Survey of India 2017).

At the regional scale, a seven-year study of fire occurrence across a gradient of vegetation types in the Nilgiri Biosphere Reserve found that moist deciduous forests had a fire return interval (FRI) of 20 years. In dry thorn scrub, FRI was 10 years and in TDDF it was 6 years (Kodandapani et al. 2008). The grass-dominated understorey in TDDFs and build-up of leaf litter creates ideal conditions for the occurrence of low-intensity surface fires; canopy fires rarely occur (Sukumar et al. 2005; Mondal and Sukumar 2016). In dry thorn scrub forests, fuel accumulation is mainly dependent on short grasses as litter accumulation is patchy and discontinuous, but the contribution of grass to fuel load is half that of TDDF (Kodandapani et al. 2008).

Increasing frequency and extent of fire was found to alter structure, composition and regeneration in these forests (Figure 2). Moderate to high fire frequency in TDDF reduced species diversity by 50-60% compared to stands with low fire frequency (Figure 2). Species diversity reduced in burned plots of moist deciduous forests by 8% compared to unburned plots. Fire reduced the density of trees (≥10 cm dbh), seedlings and saplings (5-10 cm dbh) in TDDFs and moist deciduous forests (Figure 2).

Major forest types in the Mudumalai National Park. A - tropical semi-evergreen; B - tropical moist deciduous; C - tropical dry deciduous D - tropical dry thorn (Photo: Sandeep Pulla)

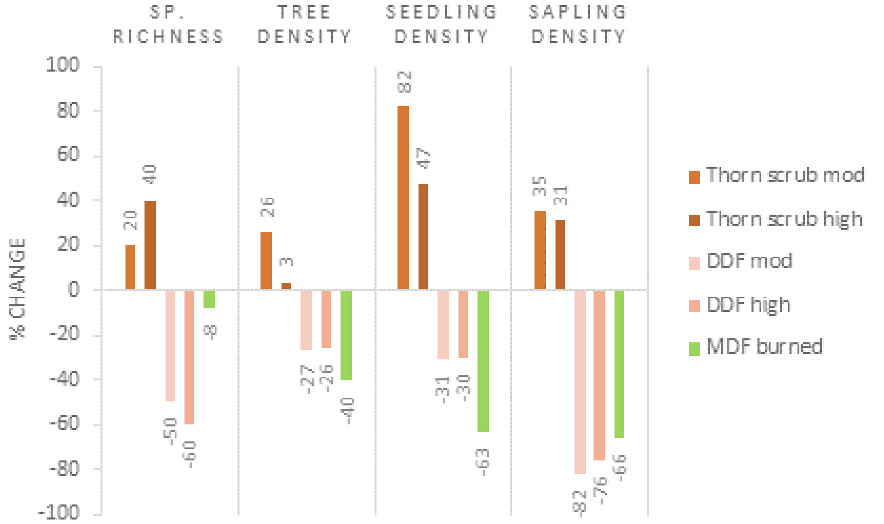

Figure 2. Response of forest structure and composition to increasing fire frequencies (moderate and high) in tropical dry deciduous forest (TDDF) and dry thorn scrub forests, relative to low-frequency fire stands, as well as in burned moist deciduous forest (MDF) compared to unburned stands. Based on data presented in Kodandapani et al. (2008).

In dry thorn scrub forests, fire had the opposite effect, increasing diversity by about 20-40% as well as increasing tree, seedling and sapling densities (Figure 2). At the landscape scale in Mudumalai, the positive influence of mean annual precipitation on woody species diversity is modulated by fire frequency – with the action of fire resulting in decreased diversity mainly through a reduction in the number of individuals and through the loss of fire-intolerant species (Dattaraja et al. 2018). The long-term consequences of such a fire regime across a regional or local rainfall gradient form a U-shaped pattern in woody plant diversity, with the lowest diversity in the intermediate rainfall zone and higher diversity in both low and high rainfall zones (Dattaraja et al. 2018).

The long-term data from the MFDP clearly demonstrate the strong influence of fire in suppressing recruitment and increasing mortality in TDDFs. Mortality tends to increase greatly in high-intensity fire years (Suresh et al. 2010). Fire was the main cause of death for smaller stems, accounting for 15% of annual mortality in the 1-10 cm dbh size class between 1988-1996 (John and Sukumar 2004; Sukumar et al. 2005). Lower average annual recruitment rates were also recorded in fire years (2.2%) compared to non-fire years (6%) (Sukumar et al. 2005). Finally, there is evidence that fire could counteract the negative effects of density dependence in some common species, thereby reinforcing their dominance in the community (John and Sukumar 2004).

The extent to which native vegetation is adapted to the occurrence of fire influences the qualitative impact of fire on forest dynamics. For instance, in seasonally dry tropical forests, many species have thicker barks, the ability to regenerate vegetatively from below-ground structures, episodic recruitment and rapid juvenile growth rates to take advantage of non-fire years (Sukumar et al. 2005). In such forests, the occurrence of fire is an integral part of ecosystem functioning and helps maintain the structure and composition of the forest (Tewari et al. 2014).

In contrast, fire has largely negative, disruptive impacts on tropical rainforest vegetation that tend to degrade rather than maintain the system by increasing mortality of large trees, opening up the canopy and reducing recruitment of native species, thereby altering species composition and successional trajectories (Elouard et al. 1997; Laurance et al. 2011). In Indian forests, vulnerability to fire is increased by ubiquitous human activities such as logging, grazing and collection of NTFPs (Kodandapani et al. 2004). Hence, some degree of management intervention is required to conserve forests from the effects of very frequent or intense fire, especially in the case of tropical evergreen and semi-evergreen forests.

The Role of Invasive Species

Invasive species can have multiple profound impacts on forest structure (Kohli et al. 2009; Bhatt et al. 2012), dynamics (Galbraith-Kent and Handel 2008) and function (Vilà et al. 2011; Wardle et al. 2011; Pyšek et al. 2012). These include reduced native species diversity (Vilà et al. 2011), altered nutrient cycling (Liao et al. 2008), modified disturbance regimes (Pyšek et al. 2012) and altered interspecific interactions such as competition with native species for resources (Gentle and Duggin 1997), and possibly also for pollinators and dispersers (Aravind et al. 2010). They can also affect the structure and dynamics of trophic webs in forests (McCary et al. 2016).

Reports on occurrences of invasive species in India date back to the late 1800s. However, research on how invasive species are changing Indian forests is still nascent – more than 60% of all studies on invasive species in India were published after 2000 (Hiremath and Sundaram 2013).

Lantana camara (lantana) and *Chromolaena odorata* are among the most abundant invasive species in seasonally dry tropical forests (Tewari et al. 2014). Here we focus on lantana as it is one of the most prevalent invasive species in Indian forests and also the best-studied (Hiremath and Sundaram 2013). Lantana invasion increased greatly in southern Western Ghats forests between 2001 and 2010. This coincided with a three-year drought starting in 2000 and widespread fires in 2002 (Sundaram and Hiremath 2012; Ramaswami and Sukumar 2013a).

In the MDFP, lantana biomass increased from 40g/m^2 in 1990 to 615 g/m^2 in 2008. The most rapid phase of expansion occurred between 2002 and 2004, following an intense fire that occurred after a prolonged drought (Ramaswami and Sukumar 2013a). Changes in lantana abundance over this 18-year period were found to be linked to an interaction between rainfall and occurrence of fire. In low rainfall years, lantana was more likely to increase in abundance if there had been a fire. Therefore, the simultaneous occurrence of drought and fire tends to increase the spread of lantana in seasonally dry tropical forests (Ramaswami and Sukumar 2013).

Grass cover was found to be much lower under very dense thickets of lantana in the MFDP (Ramaswami and Sukumar 2013b). While recruitment of several native species in the 50 ha plot did not seem to be affected by lantana density, some dry forest species such as *Catunaregam spinosa* showed lower growth rates under dense lantana thickets (Ramaswami and Sukumar 2013b). Ramaswami and Sukumar (2011) also found that mammal-dispersed woody species had lower abundances under dense lantana thickets, possibly indicating impacts on disperser communities. There is some evidence that the lantana invasion could be altering trophic interactions in seasonally dry tropical forests by affecting the quality and abundance of forage for large herbivores (Prasad 2010). The rapid increase in biomass of lantana and its replacement of grass species in the understorey of the MDFP (Tewari et al. 2014) could have implications for the fire regime in these forests (Hiremath and Sundaram 2013), nutrient cyclingand above- and below-ground carbon storage (Liao et al. 2008). Sharma and Raghubanshi (2009) found differences in litter quality and turnover under lantana thickets that correlated with altered nitrogen cycling, while Bhatt et al. (1994) found total nutrient content (N and P) of soils in lantana shrubland was lower compared to adjacent forests in Kumaun Himalaya.

The mechanisms behind observed changes in forest structure and species composition, and the overall degree to which invasive species are driving changes in forest dynamics in India are not clear at present and need further investigation.

Climate Change Factor in Driving Forest Dynamics

Indian forests have experienced an estimated temperature increase of 0.56°C over the last century. In addition, there has been a generally decreasing trend in rainfall, with reduced seasonal mean rainfall and an increase in the number of monsoon break days. There has also been a decrease in the number of light and moderate rainfall events and an increase in the frequency of extreme precipitation (Christensen et al. 2013).

Climate models under the Coupled Model Inter-comparison Project (CMIP), using the current set of potential radiative forcing-based GHG emissions scenarios (http://sedac.ipcc-data.org/ddc/ar5_scenario_process/RCPs.html), indicate that under the more moderate Representative Concentration Pathway (RCP) 4.5, the Indian subcontinent will undergo a warming of 1-2°C (compared to the 1961-1990 baseline) by 2030. Warming is predicted to be greater (2-3°C) in the Himalaya and north-western regions (Chaturvedi et al. 2012). Projections for the end of the century under RCP 4.5 range from 2-3°C for most of India, with up to a 5°C increase in the Himalaya.

Lantana *growing up the tree (Photo: Bharath Sundaram)*

Under the extreme RCP 8.5 scenario, by the end of the century, temperature could increase by 5°C for most of the country with Himalayan warming approaching 7°C (Chaturvedi et al 2012). Despite recent declining trends in rainfall, models predict an increase in the mean and extremes of rainfall during the Indian summer monsoon besides an increase in inter-annual variability (Christensen et al. 2013). Overall, precipitation is predicted to increase by 6-14% later this century (Chaturvedi et al. 2012).

*Gaur (*Bos gaurus*) grazing amid Lantana (Photo: Bharath Sundaram)*

The monsoon is projected to have an earlier onset and later retreat and last longer (Christensen et al. 2013). Model predictions for future changes in rainfall are more variable and quite uncertain compared to those for temperature (IPCC 2013).

Studies using dynamic global vegetation modelling techniques indicate that future climate change will have a large impact on Indian forests, threatening more than a third with transition from one type to another (Ravindranath et al. 2006; Chaturvedi et al. 2011; Sharma et al. 2017). The most recent study indicates that 49-54% of Indian forests (under RCP 4.5 and 8.5 respectively), could be highly vulnerable to climate-driven change by the end of the century (Sharma et al. 2017). Forests in central and south-eastern India, western Himalaya and central Western Ghats are projected to have extremely high levels of vulnerability to future climate change (Sharma et al. 2017). Among major forest types, tropical dry deciduous forests are estimated to be the most inherently vulnerable to climate change, based on canopy closure and current levels of disturbance and fragmentation, compared to tropical moist deciduous and semi-evergreen forests (Sharma et al. 2017). This conclusion is supported by another recent study which used a different modelling approach and found that drier and temperate forest types are more likely to undergo transitions under future climate scenarios (RCP 4.5 and 8.5) by the end of this century (Rasquinha and Sankaran 2016). The authors found biomes in the east-central and northern parts of the country to be most at risk from future climate change.

Climate change could affect forests directly through increased temperatures, altered precipitation patterns, increased frequency of extreme weather events and elevated atmospheric CO_2 concentrations. The indirect effects could include increased risk of fires and pathogen outbreaks (Settele et al. 2014). Effects of long-term change in temperature and rainfall could be expected to lead to the accumulation of gradual changes in forest dynamics, while extreme events would result in more drastic changes over shorter time frames.

In addition, the effects of ongoing climate change interact with other global change factors such as LULCC, spread of invasive species and nitrogen deposition (Settele et al. 2014). This leads to considerable complexity and difficulty in disentangling effects of various drivers and attributing observed changes to climate change. Further, the profound degree to which tropical tree demography is influenced by environmental stochasticity (at decadal time-scales) has recently been demonstrated (Chisholm et al. 2014). This makes the detection and attribution of directional change in tropical forest dynamics very challenging indeed, even in places where monitoring efforts span 30 years (Anderson-Teixeira et al. 2015).

Potential Effects of Increased Temperature on Tree Growth

It is speculated that tropical species may be particularly vulnerable to temperature increases as they tend to have relatively narrow thermal tolerances (Settele et al. 2014). Eddy covariance research and studies on plant physiology indicate that rising air temperatures could impact rates of photosynthesis and tree growth in tropical forests (Settele et al. 2014). Clark et al. (2010) found that increased night-time temperatures significantly increased tree mortality in lowland Neotropical forests. Tree growth was found to be quite sensitive to small variations (1-2°C) in mean annual night-time temperature. Reduction in growth rates due to increased night time temperatures causing higher respiration rates was also found across multiple Neotropical and Paleotropical rainforest CTFS-ForestGEO sites (Anderson-Teixeira et al. 2015). However, a study using experimental controlled-environment chambers, found that increased night-time temperatures led to a twofold increase in the growth rate of seedlings of two Neotropical rainforest pioneer species (Cheesman and Winter 2013).

There is some evidence that increasing temperatures may shift tree carbon allocation to increased reproduction. Pau et al. (2013) found that a long-term trend of increasing flower production in seasonally dry and evergreen tropical forests in Panama was driven by increasing temperature.

Implications of Changes in Rainfall Amount and Seasonality

Seasonality in tropical forests is driven by the quantity and distribution of annual rainfall received. As several long-term studies have now shown, variability in precipitation drives patterns of tree growth, recruitment and mortality (Suresh et al. 2010; Anderson-Teixeira et al. 2015), as well as the occurrence and magnitude of other agents of environmental stochasticity such as fire (Mondal and Sukumar 2016) or insect herbivores (Murali and Sukumar 1993). In tropical rainforests, severe drought has been shown to suppress photosynthesis and increase tree mortality by shifting tree carbon allocation towards maintaining growth at the expense of tissue maintenance and defence (Doughty et al. 2015).

Despite high inter-annual variation in rainfall in the MFDP over a 25-year study period, the potential for precipitation-driven directional change in dynamics was detected in this system. Specifically, the four-year drought between 2000 and 2004, during which rainfall was 20-40% below normal, was found to strongly affect several aspects of forest dynamics. Tree mortality increased compared to normal rainfall years, especially for species with deeper water uptake strategies (Suresh et al. 2010; Chitra-Tarak et al. 2018). This could be attributed to the depletion of water in the deeper compartments of the below-ground vadose layer. Such depletion was detected after only one year of drought and was complete by the second year of the drought (Chitra-Tarak et al. 2018). An increase in the severity and frequency of drought could potentially trigger large shifts in community composition in tropical dry deciduous forests, towards species that have shallower roots and better able to survive (Chitra-Tarak et al. 2018). The drought in 2000-2003, has also been implicated in the exponential increase in *L. camara* across vast stretches of natural forest in the southern Western Ghats (Ramaswami and Sukumar 2013a).

Apart from increased tree mortality and shifts in community composition, increase in drought frequency and severity and interaction of droughts with LULCC could alter disturbance regimes in tropical forests (Allen et al. 2010; Settele et al. 2014), making rainforest and moist forests more vulnerable to fire (Laurance et al. 2011; Mondal and Sukumar 2016). Increased tree mortality (due to drought) could open up the canopy and thin stands, rendering rainforest interiors more susceptible to fire (Settele et al. 2014). There is strong evidence that forest fires are becoming more frequent and intense due to the interaction between extreme drought and LULCC (Settele et al. 2014).

Timing and duration of early dry season rainfall affects the moisture content of forest fuel loads (Mondal and Sukumar 2016). Hence, a reduction in dry-season rainfall combined with normal or heavier wet season rain could increase the risk of fire across seasonally dry tropical forests. In dry thorn scrub forests, increased annual average rainfall, could increase fuel load and therefore the extent of burning, with implications for community dynamics (Mondal and Sukumar 2016).

Research from the MFDP shows that emergence and abundance of insect herbivores are positively correlated with annual rainfall (Murali and Sukumar 1993). The phenology of trees in dry deciduous forests is also closely linked to the onset of rainfall. Most trees begin flushing leaves in February or March (during the dry season), and peak two months prior to the peak in rainfall (Murali and Sukumar 1993). Increases in amount and duration of rainfall under climate change could increase insect abundance, while earlier onset of wet-season rainfall could increase exposure of young leaves to herbivore damage. Studies from temperate forests demonstrate how climate change-related insect and pathogen outbreaks can further increase vulnerability of forests to fire and trigger large-scale forest dieback (Kurz et al. 2008).

There is increasing evidence that climate change, interacting with other global change factors such as LULCC, could generate large-scale changes in forest ecosystems through positive feedbacks between the action of extreme drought, intense fire and pathogen outbreaks (Settele et al. 2014)

Implications of Climate Change for Carbon Stock Changes in Forests

While it is generally agreed that terrestrial vegetation has been a net carbon sink in recent decades, there are several uncertainties of the key mechanisms and processes involved as well as the future of this terrestrial carbon sink. Tropical forests were believed to be approximately carbon neutral with the growth of intact and regenerating vegetation broadly sequestering the amount of carbon lost from deforestation and degradation (Mitchard 2018). This scenario may however not play out in the future for a variety of reasons – continued deforestation, degradation and a reduced ability of tropical forests to fix carbon at current rates under future climates.

Tropical forests account for a large proportion of the forest carbon sink; however, they are also undergoing the greatest degradation and land-use and land cover change (LULCC) and therefore pose enormous uncertainty with regard to current and future carbon fluxes (Pan et al. 2011; Brienen et al. 2015). Recent pantropical, remotely sensed measurements of aboveground live woody biomass density indicate that between 2003 and 2014, tropical forests may have actually been a net source of carbon, with losses due to degradation and deforestation (~862 TgC yr^{-1}; 68.9% due to degradation), exceeding gains by 49% (Baccini et al. 2017).

Apart from the effects of degradation and LULCC, there are signs that the strength of the forest carbon sink in relatively intact tropical forests is also declining (Settele et al. 2014; Brienen et al. 2015). Several global factors interact to influence the strength of the terrestrial carbon sink, including forest regrowth, effects of changes in temperature and rainfall on carbon sequestration, altered disturbance regimes, elevated atmospheric CO_2 concentrations, and nitrogen deposition (Settele et al. 2014). Studies on basin-wide biomass dynamics in Amazonian rainforests over 30 years indicate that rates of aboveground biomass increase have declined by a third in the last decade. This is being driven by an increase in mortality rates since the early 1990s and a levelling-off of productivity since 2000. It is speculated that the increasing trend in mortality could be due to the fact that trees are growing bigger faster, increasing vulnerability to size-related risks at earlier stages of development (Brienen et al. 2015). Therefore, rates of carbon turnover in intact tropical forests seem to be increasing, affecting ecosystem net carbon accumulation. Severe drought has also been shown to reduce the Amazonian carbon sink by suppressing photosynthesis and increasing tree mortality (Doughty et al. 2015).

The carbon stock in the biomass of Indian forests has been estimated at 3070 Tg C in the year 2013 (Reddy et al. 2016). There are already clear indications that Indian forests have lost carbon stocks to the tune of −54

Photo: Arundhati Das

Tg C yr^{-1} between 2005 and 2013 (Reddy et al. 2016); though much of this seems to be related to land use change (e.g. shifting cultivation in forests of the northeast) and forest degradation, it is unclear if a changing climate has also played a role in carbon loss. This again brings out the importance of systematic monitoring of India's forests to assess the impact of climate change on biodiversity and carbon stocks.

CONCLUSIONS

At present, apart from one or two sites in the country, we have a limited understanding of the long-term dynamics of Indian forests. Studies from the Mudumalai landscape indicate that amount and seasonality of precipitation is a major driver of forest dynamics, through its effects on species diversity, tree growth and mortality and influence on the frequency and intensity of fire. Further, the impacts of drought and fire appear to vary based on the traits of the dominant species in these communities. The extent to which findings from the MFDP are generalizable to other Indian forests is not known. The large latitudinal gradient in climate as well as the sharp longitudinal gradients in precipitation in mountainous regions such as the Western Ghats generate a diversity of vegetation types with varying structure, composition, seasonality and disturbance regimes. Therefore, there is a need to replicate vegetation dynamics studies across environmental gradients in a range of biomes in the country, to evaluate the generality of findings and to draw conclusions about current and future biomass dynamics, carbon sequestration and climate change mitigation at the regional and subcontinental scales.

The great temporal variability in the dynamics of tropical forests combined with the fact that they are simultaneously experiencing the effects of multiple interacting global change factors (e.g. climate change, invasive species, defaunation, habitat degradation and loss and nitrogen deposition), challenges our ability to detect, attribute and predict the impacts of climate-driven change. Therefore, sustained long-term monitoring studies are necessary to understand how climate change is altering these ecosystems and the services that flow from them. There is also a need to combine observational studies with experimental and modelling approaches to assess vulnerability to future climate change (Settele et al. 2014).

To address some of these knowledge gaps, the Ministry of Environment, Forest and Climate Change has proposed to establish the Long-Term Ecological Observatories (LTEO-India) network as a part of the Climate Change Action Programme of India. The proposed network of LTEO-India sites will cover major Indian biomes and incorporate ecological and social perspectives in an effort to understand the complex biophysical and anthropogenic drivers of change at multiple spatial and temporal scales. With regard to monitoring of long-term forest dynamics, clusters of permanent plots would be established at these sites in all major forest types, following international protocols. The purpose of such plots would be to monitor tree growth and understand how plant demography varies by species and over time in response to change in temperature, rainfall and disturbance regime, and how these processes scale up to regulate the accumulation of forest biomass.

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Impact of Climate Change and Small Ranges on Frogs

S.P. Vijayakumar

Ingerana charlesdarwini *(Photo: S.P. Vijayakumar)*

Climate change is predicted to have significant impacts on biological diversity in montane regions across the world (Lavergne et al. 2010). One way this can happen is through its negative impacts on the geographical range of species. With warming climate, an increasing number of studies have documented upward shifts along mountain slopes in different taxa (Freeman et al. 2018). A shift in species' geographical ranges will result in significant changes in patterns of species overlap in space, potentially leading to a reassembly of major montane communities; predator-prey interactions, an imbalance in species composition and population-level changes may all occur (Bastille-Rousseau et al. 2018). Species in the mid-elevations are also expected to expand their ranges to higher elevations, resulting in significant range collision with montane species. Since there is limited area for dispersal – depending on the geographical context – in the mountaintops, it is anticipated that species will become restricted to refugial pockets, and in the absence of favorable habitats, could face local extinction.

The impact of climate change is expected to be severe on vertebrates such as frogs (Nowakowski et al. 2017), which are characterized by small ranges in the high elevations of tropical mountains. These narrow endemics are at considerable risk of range reduction and extinction. Studies in mountains like the Western Ghats in peninsular India have highlighted the existence of numerous range-restricted species in the high elevations (Biju et al. 2011). Most species are endemic to a single mountain (Vijayakumar et al. 2016). The Western Ghats houses more than 200 species of frogs (Dinesh et al. 2017), and include a number of large radiations such as bush frogs (*Raorchestes*) (Vijayakumar et al. 2016) and night frogs (*Nyctibatrachus*) (Van Bocxlaer et al. 2012) with a large number of endemics in the high elevations and montane regions. The mountains of the Eastern Himalaya are equally diverse, but the diversity of range-restricted species remains poorly explored. The patterns in islands such as Andaman and Nicobar archipelago deserves a special mention. Many insular frog species are expected to be single island endemics, and within larger islands, a few known species are restricted to small ranges. Climate change impacts are expected to be even more severe than mainland montane areas, and many small range species can face range reduction and potential extinction (Warren et al. 2018).

While the effects of climate change on range-restricted species that occur within montane areas and islands – with limited geographical space for dispersal – are likely to be severe, there are several other factors that could influence or exacerbate their condition. Large-scale human-modified landscape changes have occurred in these regions. Due to favourable climatic conditions for cash crops and the construction of large dams, vast tracts of natural forests and grasslands have been cleared and fragmented. This could pose significant barriers for species dispersal and could have negative impacts on range expansion (Guo et al. 2018). While lowland species have large ranges relative to montane species, the geographical ranges of frogs are still small in comparison to other vertebrates. We have a limited understanding of how these species may respond to changing climate scenarios.

Climate change is a major biogeographic experiment orchestrated by humans, and how frogs in different regions are going to respond is unknown. The only path towards a meaningful understanding is through tracking these changes and documenting their geographical footprint. Mountains in the Western Ghats, Andaman and Nicobar archipelago and Eastern Himalayan regions are all ancient repositories of unique evolutionary species of different ages from young to old. These species are descendants of ancestral lineages with biogeographical and evolutionary links with other ancient landmasses such as Gondwana. They are a rich repository of the history of landscapes, mountains, and regions in which they occur. Extinction of these species is an erasure of the long and rich biogeographic history of our region.

Raorchestes resplendens - *A narrow-range endemic bush frog, restricted to the montane zone of the Anaimalai massif in the Western Ghats. The questions are: can it adapt or find a suitable range in the coming decades? Or will climate change push it to the brink? (Photo: S.P. Vijayakumar)*

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Climate Change Impacts on Coastal and Marine Ecosystems

**Naveen Namboothri, Rohan Arthur,
Vardhan Patankar and Tanmay Wagh**

Coral reef in Havelock, Andaman (Photo: Rotoks; Wikimedia Commons)

INTRODUCTION

Oceans harbour multiple ecosystems and habitats that in turn harbour a large number of organisms. These organisms provide goods and services that are worth trillions of USD per year (Costanza et al. 2014; Burrows et al. 2014). Some of the key services that oceans provide are nutrition and protein for millions (including the coastal poor), jobs through tourism and fisheries, energy (oil and gas, wind, wave, tidal, thermal), protection from coastal natural disasters, regulation of weather and climate, cultural services including recreational, educational, aesthetic, and spiritual services, marine transportation and trade, and nutrient cycling and primary production (Hoegh-Guldberg et al. 2014). The monsoon rains the country receives, on which the food production of our entire nation depends, are driven by temperature and pressure anomalies between the land and sea (White 2008). More than 4 million fishers in India directly depend on the oceans for their livelihoods, and probably thrice as many on the associated economy.

Oceans and climate are inextricably linked and recent research clearly indicates that oceans are key regulators of global and local climate. Complex interactions between the three main components of our planet – the air, land and sea – result in the climate as we observe and experience today. However, humans have only recently begun exploring and understanding how oceans influence our survival. In today's world, there is a general consensus that human activities have accelerated climate change at an unprecedented rate that can have severe consequences for life on our planet (Harley et al. 2006; Hoegh-Guldberg and Bruno 2010). While climate change and its effects are becoming increasingly perceived and understood on land, its effects on our oceans and how the resulting changes in turn affect humankind remains poorly understood.

In this chapter, we review recent developments in our understanding of how climate change affects our oceans, the biota that live therein and how these impacts could in turn affect humans. We also discuss potential challenges and issues specific to India in undertaking collective action to address the climate change crisis. While the impacts of climate change on coastal and marine systems act at regional or global scales, their effects are often perceived, studied and examined at local scales.

EFFECTS OF RAPID WARMING AND TEMPERATURE ANOMALIES

Global analyses of surface air temperature (SAT) show an increasing trend (Xie et al. 2010) albeit with regional variations. Models exhibit relatively high confidence in predicting that sea surface temperature (SST) changes have closely reflected the SAT predictions (Xie et al. 2010). It is the upper layers (0-700 m) of the ocean that closely follow these patterns (Larnicol et al. 2006). Observations of SSTs over a sixty-year time period (1950–2016) indicate that the surface of three major ocean basins (the Indian, Atlantic and Pacific) have warmed over the period by 0.11°C, 0.07°C, and 0.05°C respectively (Hoegh-Guldberg et al. 2014). The vast Indo-Pacific waters are expected to undergo the highest warming in comparison to other oceanic systems, and the Northern Hemisphere is expected to warm faster than the Southern. Increase in SST is expected to be more pronounced in higher latitudes and there is evidence that isotherms are travelling to higher latitudes at rates of up to 40 km per year (Burrows et al. 2014; García Molinos et al. 2015). Long-term observations also indicate a significant increase in the frequency of marine heat waves (Oliver et al. 2018).

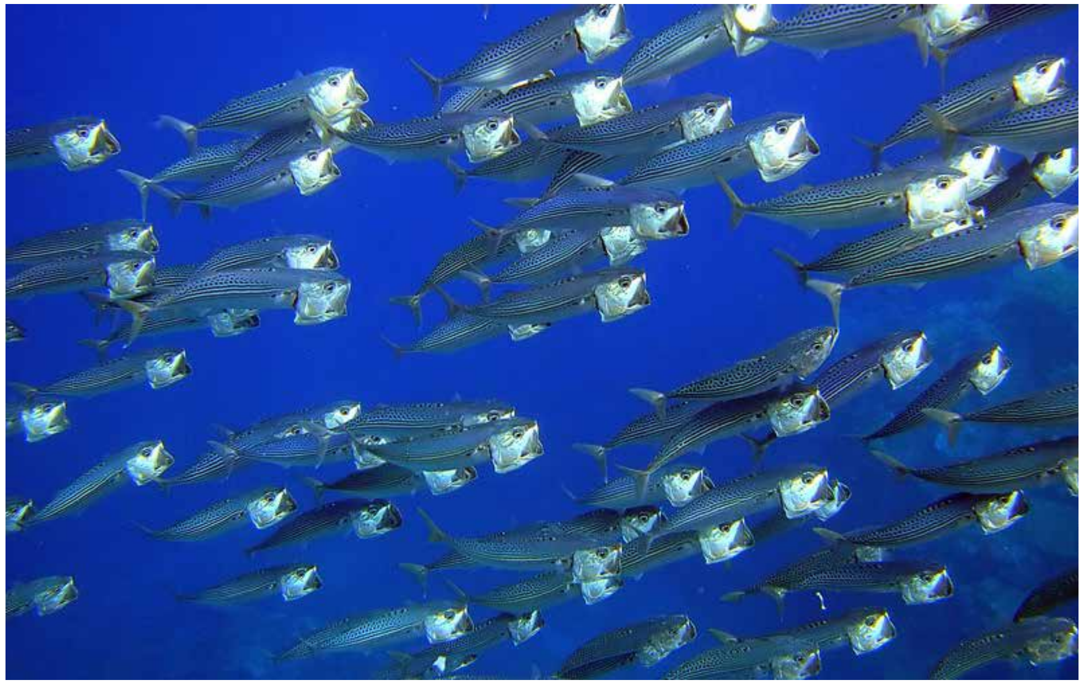
Variations in SST are also affecting ocean climate events such as the El Niño Southern Oscillations (ENSO), which is now expected to become increasingly intense. Warmer surface waters are increasing the intensity of storms, leading to greater rates of inundation of coastal regions. Coupled with sea level rise, SST variations can have significant impacts on low-lying coastal areas. Disruptions in the land-sea temperature gradients (warm ocean surface interacting with warming continents) can strengthen upwelling systems, particularly the eastern boundary upwelling systems such as the Benguela, Canary and Humboldt currents (Bakun 1990; Wang et al. 2015). The Atlantic Meridional Overturning Circulation (AMOC), a combination or the surface and deep currents of the Atlantic, for example, has been shown to have slowed down substantially and is projected to continue doing so (Smeed et al. 2014; Rahmstorf et al. 2015). In summary, the effects of SST on marine systems is one of the most well-explored, and has many direct and indirect effects at both local and global scales – it could be one of the most damaging impacts of climate change on marine systems.

Impacts of SST on Marine Fauna

In India, average SSTs are shown to have increased by 0.2°C along the northwest (NW), southwest (SW) and northeast (NE) coasts, and by 0.3°C along the southeast (SE) coast during a 45-year period from 1961 to 2005 (Vivekanandan et al. 2009). The SSTs of the southwest coast of India alone increased by 1°C. These changes have been shown to influence not just the horizontal and vertical distribution of fish species but also the phenology and reproductive patterns of commercially important fish species (Vivekanandan 2011). The distribution of the oil sardine (*Sardinella longiceps*), which forms a significant part of India's current marine capture fisheries, was limited to the southwest coast of India until 1985. The past three decades have witnessed a strong northward shift in the distribution of the species, and they have now become a crucial part of the fisheries along the entire coastline (Vivekanandan 2011). The northward movement of the distribution ranges of sardine stocks shows a strong correlation with changes in SSTs.

The Indian mackerel (*Rastrelliger kanagurta*), a pelagic planktivorous fish, is known to prefer the shallow subsurface waters of the Indian coastline and was harvested primarily using gill nets. From 1985-1989, trawlers contributed to only 2% of their total annual catch, but this increased significantly to 15% during the 2003-2007 period. It is speculated that the fish species is undertaking vertical migrations and moving to deeper waters as a result of elevated SSTs (Vivekanandan 2010).

Vivekanandan and Rajagopalan (2009) studied the breeding biology of two species of threadfin breams (*Nemipterus japonicus* and *N. mesoprion*), which are widely distributed at depths from 10 to 100 m along the Indian coast. Data on the frequency of occurrence of female spawners of *N. japonicus* over a period of 25 years (1981 to 2004) off the Chennai coast indicated wide fluctuations. During the 1981-1985 period, 36.3% of the gravid female occurrences were during April-September (with a mean SST ranging from 29-29.5°C) and 64.9% during the relatively cooler October-March period (mean SST ranging from 27.5-28°C). This pattern shifted to 5% occurrence of female spawners during the warm months and 95% during the cooler months. *N. mesoprion* followed a similar pattern. This indicates a strong shift in spawning windows in response to warming SSTs with the fish avoiding the warmer months of April to September.



*School of Indian mackerel (*Rastrelliger kanagurta*) feeding on macroplanton*
(Photo: Dino van doorn; Wikimedia Commons)

While the sardines show a clear northward migration, the vertical migration of mackerels and the phenology changes in the breams need further validation to exclude the influences of other factors in driving the observed patterns. For instance, the drastic changes in the engine capacities, increased mid-water trawling, etc. could have led to increased mackerel catches in trawl fisheries. Similarly, it is not clear if the shift in the breeding biology of the breams is driven by climate change or other non-climatic factors.

The Future of Coral Reefs in a Warming Ocean

Corals and coral reefs are particularly sensitive to climate change-induced temperature anomalies and act as the harbingers of climate change. One of the most spectacular ecosystems on the planet, coral reefs are comparable to tropical evergreen forests in terms of complexity and biological diversity (Connell 1978). In addition to their aesthetic and biological value, coral reefs help generate revenue upwards of a few billion dollars, providing ecosystem services and livelihood support to millions world over through tourism, fishing, coastal protection and a vast array of bioactive compounds used in the pharmaceutical industry (Carté 1996). Also, as one of the most studied tropical marine ecosystems, coral reefs have provided us with profound insights into how our oceans respond to the impacts of climate change.

However, despite the direct and indirect benefits they provide humans, they are increasingly pressured by long-term, chronic anthropogenic disturbances such as pollution, sedimentation, overfishing, disease facilitation and physical disturbances. A more recently identified threat is ocean acidification (Gattuso et al. 1998; Kleypas et al. 1999). The compounded effect of these stressors have now placed one-third of the coral species of the world under extinction threat (Carpenter et al. 2008) and approximately 27% of reefs have been lost, while as much as 32% are at risk of being lost within the next two decades (Pockley 2000).

Effects of Climate Change-Induced 2016 Bleaching Event on Coral Reefs of the Andaman and Nicobar Islands: A Case Study

The reefs of the Andaman and Nicobar Islands are among the most biologically diverse reefs in Indian waters due to their geographical proximity to the Indo-Malay-Philippine Coral Triangle (Bakus et al. 2000; Roberts et al. 2002). Islanders are heavily dependent on these reefs as a major source of income through tourism and fisheries; and for coastal protection. However, our understanding of these reefs is limited to diversity and taxonomic surveys (Scheer 1971; Pillai 1983, 1996).

In the past decades, reefs of these islands have been victim to multiple catastrophic disturbances, the global mass bleaching events of 1998, 2002 and 2010 and the tsunami of 2004 (Rajasuriya et al. 2002; Krishnan et al. 2011; Patankar et al. 2012). The reefs that were showing signs of recovery from these multiple large-scale impacts were again hit by a severe and prolonged bleaching event in the summer of 2016. The rise in SST can cause large-scale mortality of coral species and have flow-on consequences for other reef organisms from invertebrates to fish (Munday et al. 2009). Further, other factors including strong surges, cyclones, terrestrial river/sediment run-off and predator outbreaks such as crown-of-thorns sea stars and human disturbances (such as increased coastal development, sedimentation resulting from poor land-use and watershed management, sewage discharge, nutrient loading and eutrophication from agrochemicals, coral mining, and over-fishing) have further degraded the reefs of these islands (Wilkinson 1999; Kulkarni et al. 2008). A combination of these factors can impact a host of ecological processes the complex reef framework provides, and the effects can trickle down to the dependent communities and consequently the island economy as a whole. This catastrophic mortality raises crucial questions about the recovery potential of these reefs, and the long-term resilience of the ecosystem to a changing climatic regime.

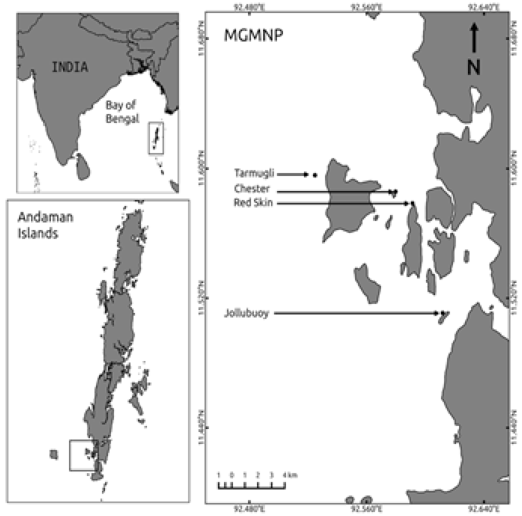


Figure 1. Map of South Andaman Islands indicating sampling location inside Mahatma Gandhi Marine National Park (MGMNP)

A long-term reef monitoring study was initiated in 2012 with support from the Department of Science and Technology at the Mahatma Gandhi Marine National Park (MGMNP) situated in the Andaman Islands, Bay of Bengal (Figure 1) to understand the impacts of climate change on reef systems. Results from surveys carried out at four islands (viz. Jollybuoy, Redskin, Tarmugli and Chester Island) in the years 2012, 2016, 2017 and 2018 along with a bleaching survey carried out in 2016 from the MGMNP are reported below (also see Figure 2).

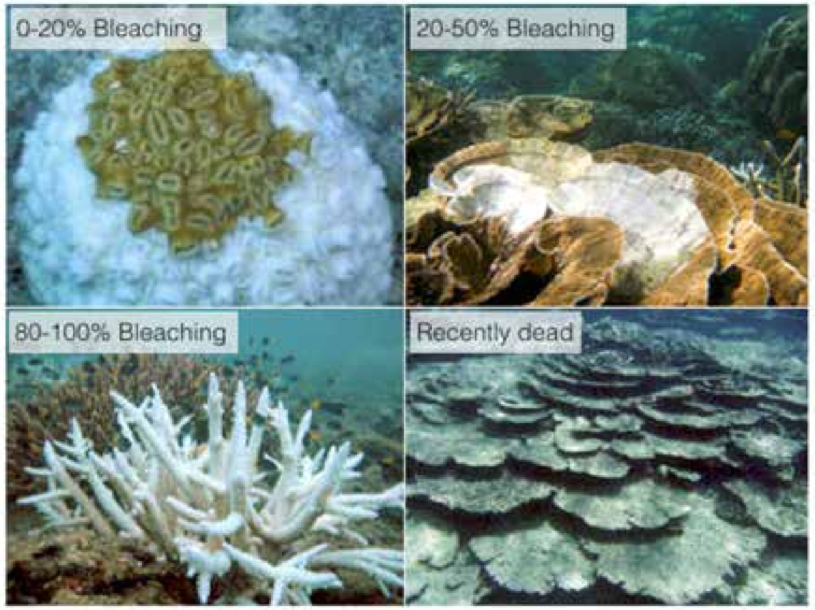


Figure 2. Various stages of bleaching used to classify coral colonies. Source: Wikimedia commons

Impacts of the bleaching of 2016 on coral communities

The El-Niño Southern Oscillation Event triggered a mass bleaching event in 2016, resulting in excess of 80% coral bleaching in the Andaman Islands (Figure 3). The bleaching intensity varied between sites as well as different genera. Branching species such as those of the genus *Acropora* were more susceptible to bleaching when compared to massive/sub-massive genera such as *Porites*. During the surveys, some colonies had already died and were covered by algal turfs underlining the rapid cascading impact of such disturbances.

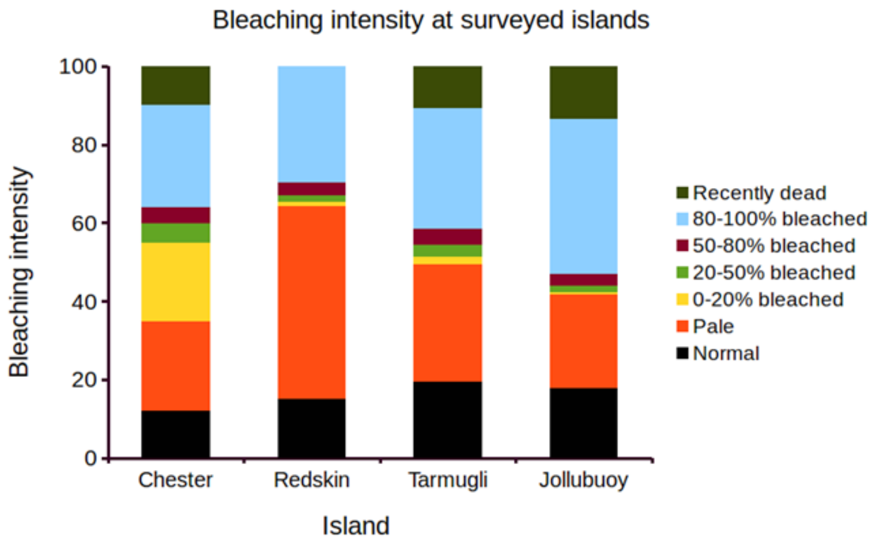


Figure 3. Bleaching intensity in terms of the number of colonies bleached across the four islands during the year 2016

Changes in live coral cover observed across the years

Live coral cover (which indicates the overall health of the reef) ranged between 30% and 35% during our first survey in 2012, and did not vary significantly between sites, indicating a certain degree of natural recovery after the 2004 tsunami and the 2010 bleaching event (Figure 4). The coral cover dropped drastically in the El Niño year of 2016, with the mean coral cover as low as 21%. However, the reefs showed remarkable recovery again in the next year, bouncing back to pre-bleaching levels of live coral. Though this pattern was observed at all four sampled sites, it was more evident in Jollybuoy and Tarmugli islands respectively (Figure 4).

Immediately after the bleaching event, we documented growth of turf algae on a few dead corals. These algae are known to inhibit coral settlement (Birrell et al. 2005) and potentially affect reef recovery. However, abundance of herbivores at most sites was a positive sign as herbivores are known to keep the surface of dead coral colonies relatively free from algae, thereby providing better conditions for new scleractinia to settle (McClanahan et al. 2001). The ability of reefs to recover, however, seems to be reducing as the mean percent cover dropped by 12% from 2017-2018. Similarly, reefs at different islands showed different responses and recovery from stresses, underlying the importance of local biotic (fish communities, algal growth, coral species composition and structural complexity) and abiotic (nutrient regimes, sedimentation, wave exposure, terrestrial runoffs, etc.) factors in promoting or reducing reef resilience.

As the frequency of benthic disturbances increases, reefs lose their inherent natural resilience to stresses which impairs the ability of corals to recover (Roche et al. 2018). This results in lowering of coral cover, a rise in algal cover and a reduction in the diversity of coral species as the community gets dominated by high resilient coral species (Hughes et al. 2018; Yadav et al. 2018). This can have cascading impacts on the reef systems as a whole, consequently affecting the dependent coastal communities.
The relatively limited anthropogenic stresses in the Andaman Islands in the past could have resulted in higher resilience of reef systems to resist and recover from cataclysmic disturbances. However, the increase in coastal developmental activities, reef fishery, sedimentation and improper sewage disposal can confound the impacts of climate change on the reefs, reducing their potential to recover. Although global policy changes are needed to reverse the impacts of climate change on reefs, managing local stressors that promote reef resilience can greatly increase the ability of reefs to bounce back from disturbances as they have shown in the past.

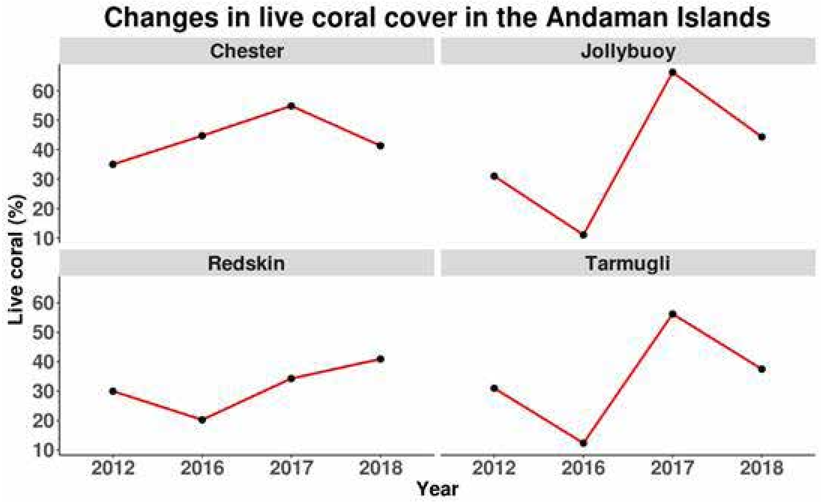


Figure 4. Plots showing the changes in the percent composition of mean live coral cover at four islands from the years 2012 – 2018

Effects of Multiple Climate Change-Induced Bleaching Events on Lakshadweep's Coral Reefs

Like other low-lying atoll islands, the Lakshadweep Archipelago are among the most vulnerable to anthropogenic climate change. The normally shallow lagoons and tiny islands are protected within a framework composed largely of biogenic calcium carbonate that is produced by living coral and coralline algae. Maintaining this biogenic growth against the forces of constant erosion is key in ensuring the atoll framework continues to provide its protective function to the islands and their inhabitants. Over the last two decades, reef growth has been compromised by a series of El Niño events that affected the Lakshadweep in 1998, 2010 and 2016. The El Niño current increases sea surface temperatures well above seasonal averages resulting in a breakdown of the symbiotic relationship between photosynthetic dinoflagellates (zooxanthellae) and scleractinian coral (dominant reef-building species). This is a condition known as bleaching, from the paling of coral as zooxanthellae abandon their coral hosts. When prolonged, this heat stress results in reef-wide coral mortality, from which the ecosystem can take years or decades to recover.

In the Lakshadweep, each subsequent El Niño event has been more stressful than the one before in temperature intensity as well as in duration. Despite the increasing magnitude of each El Niño event, long-term data from several monitored sites across the archipelago shows that the percent of coral mortality reduced with each event (Yadav et al. 2018). While 1998 saw the loss of more than 80% of corals in shallow reefs, 2016 saw a decline of a little more than 30%. This suggests that the coral assemblage of the Lakshadweep is becoming increasingly resistant to heat stress. A large part of this resistance is due to the rapid filtering-out of species that are highly susceptible to temperature stress with each El Niño, leaving behind an assemblage dominated by heat-tolerant species.

While this increased resistance may be a positive sign, post-disturbance recovery paints quite a different picture. The ability of live coral to recover after each event has declined dramatically from the 1998 event to the 2010 event, and it remains to be seen at what rate recovery will take place post-2016. Rates of recovery post the 1998 bleaching event were estimated to be 8-10 years (to recover their pre-bleaching values), while the rates measured post the 2010 bleaching event would require at least three decades to regain their pre-bleaching cover values (Yadav et al. 2018). When the declining rates of recovery is seen against the increasing frequency of global El Niño events (likely to recur every 4-5 years), the ability of the living coral to keep up rates of reef growth to match erosional rates is very much in doubt.

A suite of other studies show the consequences of this loss to the ecosystem as a whole. Worryingly, many long-lived benthic predators like groupers are unable to cope with the loss of physical structure in the wake of repeated bleaching events. Most

Some reefs are now coral graveyards in the Lakshadweep (Photo: Rohan Arthur)

continue to survive only in the most stable reefs, where the physical architecture has not undergone too much change through time (Karkarey et al. 2014). There is a large variability in response however, and while most species lose out, others like the peacock grouper (*Cephalopholis argus*) show a significant amount of adaptive potential, shifting their foraging behaviour from being an ambush predator to a roving feeder as the structure changes (Karkarey et al. 2017). Similarly, some coral-feeding butterflyfish like the Melon butterflyfish (*Chaetodon trifasciatus*) also adapt to changing conditions by becoming much less fussy about what they eat, and eating much more voraciously when they find edible coral in sparse environments (Zambre and Arthur 2018).

In another pivotal study, Alonso et al. (2015) showed that independent of everything else, disturbance events can differentially influence the natural extinction rates of fish species within the pool, with higher trophic groups (like groupers and sharks) being inherently more vulnerable to being lost than omnivores and herbivores. Clearly then, fish assemblages are responding in complex and nuanced ways to declining reef conditions, resulting in a set of winners and losers, depending on the relative plasticity of species to changing conditions.

Taken together, the trends emerging from long-term studies in the Lakshadweep point to a system declining rapidly due to rapid climate stress. The longer-term consequences of this loss for human food security and the inhabitability of the islands is an open question. The current upsurge in commercial reef fishery only worsens the impending disaster. If current trends continue, the Lakshadweep islanders could well face a bleak future – they could be forced to evacuate their islands as the atolls crumble and fish numbers dwindle.

Disruptions in Ocean Circulation

While surface currents of oceans are predominantly driven by winds, sub-surface currents are driven by a combination of temperature, density and salinity. The horizontal and vertical circulation of seawater creates a complex pattern of water movement, moving adult and larval forms of marine fauna as well as heat and nutrients, and maintaining connectivity over long distances. This is crucial in maintaining the biological and ecological integrity of our oceans, and local productivity and food production. Many fisheries, particularly upwelling-associated fisheries, for instance, survive on the predictability of winds that move large volumes of surface waters. Long-term data indicates that some wind-dependent upwelling systems could intensify under climate change (Sydeman et al. 2014; Di Lorenzo 2015) and these could have potentially positive or negative consequences (Bakun et al. 2015).

A major predicted impact of changing ocean circulations on coastal and marine fauna is by way of disrupting contemporary connectivity patterns (Toggweiler and Russell 2008). Most marine organisms, ranging from vertebrates such as tuna to invertebrates including sponges and molluscs, have a pelagic larval stage in their early life history. These larvae are carried by ocean currents connecting distant coastlines. Climate change driven reorientation of currents could lead to connecting regions that were previously unconnected, thereby facilitating the redistribution of species beyond their known ranges, leading to a reassembly of marine communities (Toggweiler and Russell 2008). The strengthening of the East Australian Currents, for instance, has facilitated the spread of the sea urchin (*Centrostephanus rodgersii*), from the Australian coast to Tasmania, where it was previously unknown (Ling et al. 2009). The arrival of this urchin has drastically reduced the distribution and abundance of kelp forests with implications for fisheries and other ecosystem services (Ling et al. 2009).

Rising Sea Levels

A slow but devastating effect of climate change on our coastlines is by way of sea level rise. Seas are expected to rise globally at a rate of 1-2 mm yr-1 with the rates drastically increasing after 2050. The International Panel for Climate Change (IPCC) estimated global sea level rise to be at 0.52-1.00 m by the year 2100 (Church et al. 2013). Melting glaciers are expected to contribute to 44% of the predicted SLR, and thermal expansion of water is expected to contribute 42% (WCRP Global Sea Level Budget Group 2018). The effect of melting of glaciers and the polar ice caps will affect sea levels globally, while thermal expansion is predicted to have more localized effects (Nicholls and Cazenave 2010).

Though levels of sea level rise on the Indian coastline are consistent with the global average (an average rise of 1.29 mm yr-1) (Unnikrishnan and Shankar 2007), given the dense population living on India's coastlines – where nearly 250 million people live within 50 km of the sea – such changes can have serious implications for coastal vulnerability (Nicholls and Cazenave 2010), particularly for low-lying coastlines such as the Lakshadweep group of islands (Unnikrishnan and Shankar 2007). The east coast of India, particularly the low lying Ganges-Brahmaputra delta, will witness severe impacts of sea level rise compounded with rapidly submerging coastlines and increased storm surges and cyclones (Shetye et al. 1991), making it one of the most vulnerable coastlines of the world.

Coastal Squeeze and its Impacts on Marine Ecosystems

Globally, coastal protection and engineering projects are squeezing coastlines from the landward side while SLR and coastal erosion due to various factors (such as reduced sediment supply, sand mining, construction of ports, breakwaters, etc.) are impacting them from the seaward side (e.g. Doody 2013). With no space to move landwards, most coastal, intertidal and shallow subtidal ecosystems such as coastal sand dunes, mangroves, salt marshes, intertidal sandy beaches, rocky shores, shallow coral reefs and seagrass meadows are susceptible to large-scale habitat loss. Vast coastal stretches along the Indian coastline have already been lost to coastal infrastructure projects and coastal armouring (Namboothri et al. 2008). New projects such as the ambitious 'Sagarmala project' (http://sagarmala.gov.in/) that aim at building a port-based economy and involve massive infrastructure development along the entire coastline of India need to consider the issues of 'coastal squeeze' on the health of coastal and marine ecosystems.

Mangrove Submergence

Mangrove forests grow at the interface of land and sea and have evolved adaptations to survive in these dynamic, harsh conditions. Mangroves are also habitats for specially evolved organisms ranging from birds to invertebrates such as crustaceans and molluscs, and nurseries for the juveniles of many economically important species. They provide fuelwood for local communities, add to local productivity by supplying large quantities of nutrients and protect the hinterland from the vagaries of the seas. Despite their crucial roles, mangrove ecosystems globally have been on the decline, the most significant contributor of this decline being unsustainable development practices associated with economic development and population pressures in the tropics. Limited in their distribution, the sixty odd species of mangroves cover an area of approximately 170000 km^2.

In addition to localized anthropogenic pressures, mangroves are prone to the effects of climate change, the most critical of them being sea level rise (Field et al. 1998). With increasing pressures from the landward side limiting their distribution, mangrove systems are expected to be affected the most by the coastal squeeze as they struggle to keep pace with changing sea-level. Mangrove ecosystems evolve over centuries, if not more, arriving at a synchrony between the flora, fauna and the physical environment. When sea level rise is faster than the rates at which sediment deposition happens and the rates at which mangroves can expand landwards, they invariably face the threat of submergence. This will be particularly severe on low-lying, carbonate-heavy settings, such as those found on many oceanic islands that lack rivers (which will be the most prone to sea-level rise because of their sediment-deficit environments) (Ellison and Stoddart 1991). Reconstruction of past mangroves and their adaptations to sea level rise have indicated that mangroves have survived SLR at rates of 8-9 cm/100 years by spreading landward (Ellison and Stoddart 1991; Ellison 1993), and current rates of SLR are predicted to be much lower. However, with little space available for landward expansion, such opportunities for expansion and survival may not be available for contemporary mangroves. While some researchers have predicted that mangroves will probably survive climate change impacts better by moving poleward (Alongi 2015) this may not be the case for all species of mangroves.

OCEAN ACIDIFICATION

Oceans have absorbed about a third of the total anthropogenic CO_2 over the past 200 years (Sabine et al. 2004). While oceans have helped moderate CO_2 levels and slow the rate of climate change, this has come at the cost of large-scale changes to ocean chemistry. The excess CO_2 entering seawater decreases the pH of the water, making it more acidic than normal and leading to a range of large-scale chemical changes collectively known as ocean acidification (Orr et al. 2005). Acidic conditions reduce the calcifying ability of species and in turn, their ability to make their calcium carbonate skeleton (Hoegh-Guldberg et al. 2007). Though the topic has not received the kind of sustained attention that other climate change impacts have, ocean acidification is now increasingly identified as a process that could cause irreversible damage to marine systems at the global scale (Doney et al. 2009).

Since the industrial revolution that triggered the sudden increase in greenhouse gas emissions, the average pH of the ocean's surface waters has decreased by about 0.1 units – from about 8.2 to 8.1 (Havenhand et al. 2008). Even conservative estimates project an additional 0.2-0.3 drop by the end of the century (Caldeira and Wickett 2005). This apparently exceeds any known changes in the ocean chemistry over the past 800,000 years (Ridgwell and Zeebe 2005). The effects of ocean acidification – both short-term and long-term – on the organisms that inhabit the oceans are still debated. But there is a general consensus that many marine organisms – particularly ones with calcareous shells – will be affected severely, altering the services that they provide to both ecosystems and the society (Raven et al. 2005).

Thermal stress causes reefs to bleach and eventually die if the stress prolongs (Photo: Vardhan Patankar)

Plankton communities form the base of the marine food chain and many of them (particularly diatoms) rely on a calcareous outer shell for survival. Diatoms generate more than 20% of the net organic carbon that is produced globally through photosynthesis (Field et al. 1998). Acidification of the oceans can lead to significant declines of diatoms globally, and the effect of such a decline will get magnified up the food chain, which could lead to significant disruption of contemporary marine community assemblages (Rossoll et al. 2012). However, some species of phytoplankton are expected to thrive while some others will be unaffected by more acidic conditions (Dutkiewicz et al. 2015). In summary, though predictions indicate that there may be winners and losers in planktonic communities, it is certain that our oceans are going to witness a substantial change in the planktonic community structures and a much more drastic, magnified change higher up in the food chain.

For ecosystem foundation-forming groups such as corals, the predictions were gloomy a decade ago (Hoegh-Guldberg et al. 2007). The aragonite skeleton was expected to form only in an equilibrial pH condition, and it was predicted that most corals would lose their calcification ability with increasing acidification. This was expected to result in the loss of framework-building coral species, less diverse reef communities and weak carbonate reef structures – all collectively leading to eroding functionality of reef systems globally (Hoegh-Guldberg et al. 2007). Recent research, however, indicates that corals may have certain inherent biological traits in the form of highly acidic proteins that facilitate carbonate deposition in acidic conditions, thereby providing the ability to cope with changing seawater chemistry (Von Euw et al. 2017). Nevertheless, it is not clear how ocean acidification combines with other stressors like thermal anomalies, pollution, etc.; hence these effects will need to be better understood both in isolation and in combination with other climate change-related issues to predict the future of coral reefs.

The impacts of ocean acidification on coastal and marine biodiversity is poorly researched in the Indian waters. Considering the nation's major dependence on marine resources, it is imperative that immediate attention is given to this topic. India needs to set up long-term SST and acidification monitoring centres that involve both physical and biological oceanographers.

Climate Change and Dead Zones in the Ocean

Oxygen levels in seawater are crucial for sustaining life in oceans. Ocean mixing, photosynthesis, respiration and seawater solubility are the four main modes through which oxygen enters seawater (Breitburg et al. 2018). Globally, there is increasing evidence indicating that the concentrations of oxygen in oceans are declining at an alarming level. In addition to sewage and other types of coastal pollution, three climate change related factors regulate availability of oxygen in seawater – (1) strong heat-related stratification of the water column (less ventilation and mixing) (2) reduction in the oxygen dissolving potential of seawater with increasing sea surface temperature (3) impacts of warming on biological processes such as photosynthesis and respiration (Bopp et al. 2013; Pörtner et al. 2014; Shepherd et al. 2017). All of the above factors, in isolation or in combinations, can lead to significant alterations of ambient oxygen levels. Reduced oxygen levels in oceans can create 'dead zones' or areas of low oxygen levels (where oxygen concentrations have fallen below 2 ml of O2/ litre of seawater), where oxygen-breathing fauna cannot be sustained (Rabalais et al. 2002). The levels of contribution of climate change and non-climatic factors to these dead zone formations are not clear; however, it is now evident that the number of dead zones has increased globally (Diaz and Rosenberg 2008).

Diverse corals re-colonizing dead reef bottoms (Photo: Vardhan Patankar)

Coupled with ocean acidification, deoxygenation is expected to increase, particularly in areas where coastal pollution is high. Excessive organic carbon produced through the eutrophication of surface waters could reach deep benthic habitats and accelerate the decline in oxygen concentrations through anaerobic microbial activities (Breitburg et al. 2018).

Even hardy benthic species are known to be directly affected by such rapid oxygen depletion, and the spread of such zones could decimate fisheries locally and lead to severe ecological, economic and social disasters. A recent report mentions such a large dead zone formation in the Bay of Bengal leading to speculations of large-scale livelihood and biodiversity losses (Ghosh and Lobo 2017).

Prospering Coasts and Increasing Vulnerabilities

Coasts have historically been hubs for trade and economic development and continue to serve this role. The past century has seen disproportionately high infrastructure growth, development initiatives, settlements, urban centres and tourist resorts come up along the coastlines globally. Twenty-three percent of the world's human populations live within 100 km of the coast and below a 100m elevation from the sea level (Small and Nicholls 2003). Twelve of the world's sixteen cities with populations greater than 10 million are located within 100 km of the coast, many within 10-20 km. In India, 250 million people live within 50 km of the coastline. Some of the direct impacts of such rapid changes on coastlines include discharge of sewage, sediment, fertilizers and contaminants into coastal waters, degradation of coastal sand dunes and mangroves, obstruction of sediment transport and natural beach dynamics (Scavia et al. 2002; Lotze et al. 2006). In addition, growing coastal populations have also put intense pressures on fisheries resources, leading to spectacular collapses in fisheries in many parts of the world. Coastal ecosystems such as corals reefs and mangroves have undergone significant declines in the past 4-5 decades, and have severely undermined the livelihoods of the millions who depend on these resources for sustenance.

This disproportionate growth focusing on coastlines have also exposed a significant proportion of people to coastal catastrophes such as storm surges, cyclones, sea level rise and tsunamis. Coastal vulnerability is particularly high in Asian countries, where a coast-based economy is rapidly growing. Monsoon-affected Asia is one of the most cyclone-prone regions of the world and witnesses ~42% of the world's total tropical cyclones (Ali 1999). Combinations of these extreme climatic and non-climatic events (such as man-made erosion and human disruption of coastal dynamics) have caused coastal flooding, which in turn has led to substantial economic losses and fatalities (Yang et al. 2000; Yinghua et al. 2004).

Translating Knowledge into Action

The Dichotomy Challenge

Addressing the challenges of climate change is not an easy task for countries like India, which have a significant rural population with a very low per-capita consumption, who are also most vulnerable to the impacts of climate change. The rest of the Indian population comprises rapidly developing consumerist urban and semi-urban people, with higher per-capita carbon footprints, emission and consumption levels. Developing an inclusive climate action plan in an economically, socially and culturally diverse country like India is a daunting task and will have to involve collective discourse and action transcending ministries, scientific institutions, political parties and civil society organizations.

Communities that depend on natural resources (farmers, fishers, forest dwelling communities, etc.) and are by extension impacted by climate change will be the first to experience and recognise the impacts of climate change. Centuries of direct dependence on nature and climate have given them deep insights into understanding and adapting to climate change. It is important to include these communities in the larger climate debate and discourse, thereby also creating opportunities to incorporate traditional ecological knowledge into climate action. Most climate discussions take place at national, regional or global scales with little opportunity for local communities to participate and contribute. India needs to decentralise the discourse around climate change and create opportunities or platforms for rural communities to engage and participate. Institutions such as the Gram Panchayats could play a huge role in facilitating this and in creating a larger social-political movement that aims at tackling climate changes related issues from the bottom-up.

Scientific Uncertainties and Consequences

Science is still struggling to arrive at reliable estimates of the impacts of climate change on the planet and its inhabitants. While science progresses by refining and refuting previous work, new research in this complex field is prone to reversal or recalibration of previous findings. Such uncertainties are often exploited by both corporates and development planners to justify actions that could be environmentally unsustainable. The uncertainties also tend to discourage policy makers from taking bold decisions and stringent action that can have major implications for the nation’s development and economy.

The uncertainties associated with the science of climate change and the challenges in dissociating local chronic pressures from global, large-scale processes, intentionally or unintentionally, make for an effective cover for all environmental issues at local scales. For instance, upstream interventions in the flow of rivers (e.g. dams, barrages, diversion of rivers/streams, etc.) often lead to reduced sediment supply to beaches downstream, leading to severe erosion of coastlines. Interestingly, most studies on coastal erosion tend to ignore such possibilities and often end up accusing global climate change for issues created locally.

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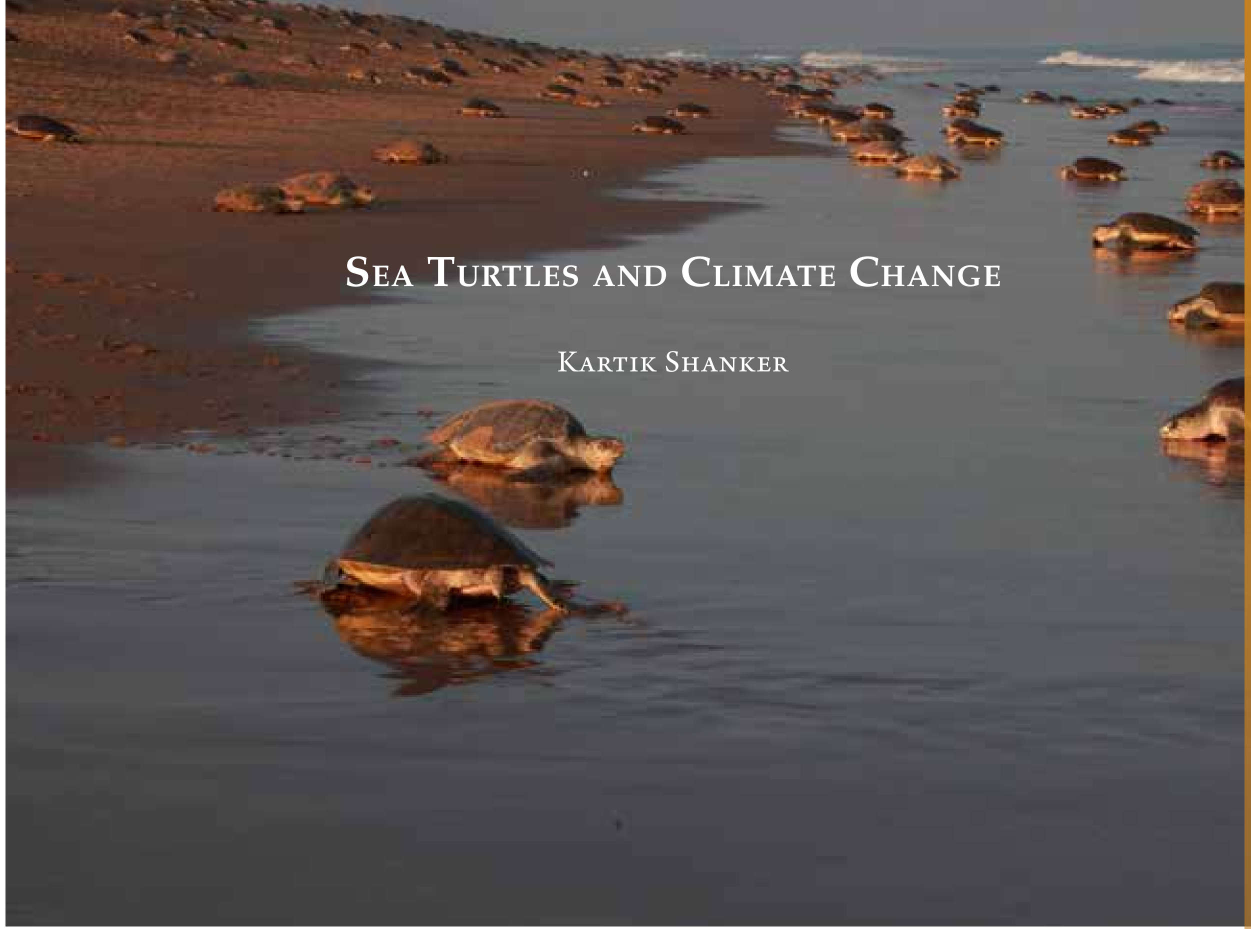
SEA TURTLES AND CLIMATE CHANGE

KARTIK SHANKER



*Olive ridley turtles (*Lepidochelys olivacea*) coming ashore during an 'arribada' (mass nesting) in Rushikulya, Odisha in 2013. The major mass nesting beaches of olive ridleys in the world are in Pacific central America and in Odisha on the east coast of India (Photo: Kartik Shanker)*

There are seven species of sea turtles globally, of which four species have significant nesting and/or foraging grounds in India. There are significant nesting beaches for leatherback (*Dermochelys coriacea*), green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles in the Andaman and Nicobar Islands. Green turtles also nest in Gujarat and the Lakshadweep Islands, which are a major foraging ground for them. Olive ridley turtles (*Lepidochelys olivacea*) nest throughout the mainland coast and islands, but the east coast of India has the highest densities of nesting. The olive ridley turtle mass nesting beaches in Odisha (at Gahirmatha and Rushikulya) are amongst the largest in the world (Shanker et al. 2004a). These have received particular conservation attention as they are the only major mass nesting beaches in the world outside of Pacific central America, and may be the ancestral source for ridleys worldwide (Shanker et al. 2004b).

Climate change can affect sea turtles through its impact on their nesting and foraging habitats (Fuentes et al. 2013). Both rising sea levels and extreme events can lead to a loss of habitat, particularly nesting beaches but also coral reefs and seagrass meadows. The loss of nesting beaches has, in particular, been identified as an immediate threat to sea turtles from climate change. However, there are also impacts on food and foraging habitats. Leatherbacks, for example, feed almost exclusively on jellyfish, and changes in ocean productivity can lead to fluctuations in the availability of food. Similarly, green turtles are herbivores, and feed largely on seagrass and algae.

Green turtles in the Lakshadweep Islands are shown to have significantly altered seagrass communities, causing species shifts and lowering densities of seagrass (Kelkar et al. 2013). Climate change could exacerbate this by influencing the resilience and recovery of seagrass meadows, thus affecting the persistence of these critical habitats for green turtles.

In addition to its impact on habitats, climate change also affects sea turtles by its influence on sex ratios through increasing temperature. Many reptiles, including sea turtles, exhibit Temperature-dependent Sex Determination (TSD) (Yntema and Mrosovsky 1980). In sea turtles, higher nest temperatures produce female hatchlings and lower temperatures produce males. Incubation temperature of clutches influences hatchling development as well as their sex. The incubation temperature, in turn, depends on external factors such as air temperature, sand grain size, and internal factors such as clutch size. A rise in air temperature is expected to lead to changes in sand temperature which would influence the sex ratio of individual clutches, and eventually lead to changes in population sex ratios, which could be detrimental to turtle populations. For example, Jensen et al. (2018) show that the northern beaches in the Great Barrier reef have been producing primarily females for two decades or more. In addition, higher temperatures could affect hatchling fitness, and even lead to mortality, both of which would have a negative impact on hatchling production from nesting beaches, and affect recruitment into populations.

While TSD has been studied in many sea turtle species, there are relatively few studies on olive ridley turtles. In India, Dimond and Mohanty-Hejmadi (1983) conducted a study which suggested a pivotal temperature at ~29⁰C, above which females would be produced. Long term monitoring of sea turtles has been carried out at the Rushikulya rookery since 2008. This has included monitoring of offshore and nesting populations as well as hatching success and sex ratios (Chandrana et al. 2017). In most years, the mean nest temperatures exceeded the pivotal temperature, which would lead to the production of more females than males. This is clearly reflected in the empirical data based on the sexing of a sample of hatchlings, where females exceed males in most years, with complete feminisation in 2016 (Figure 1). With increasing temperatures, it is expected that the production of hatchlings from the mass nesting beaches of Odisha could become completely feminised.

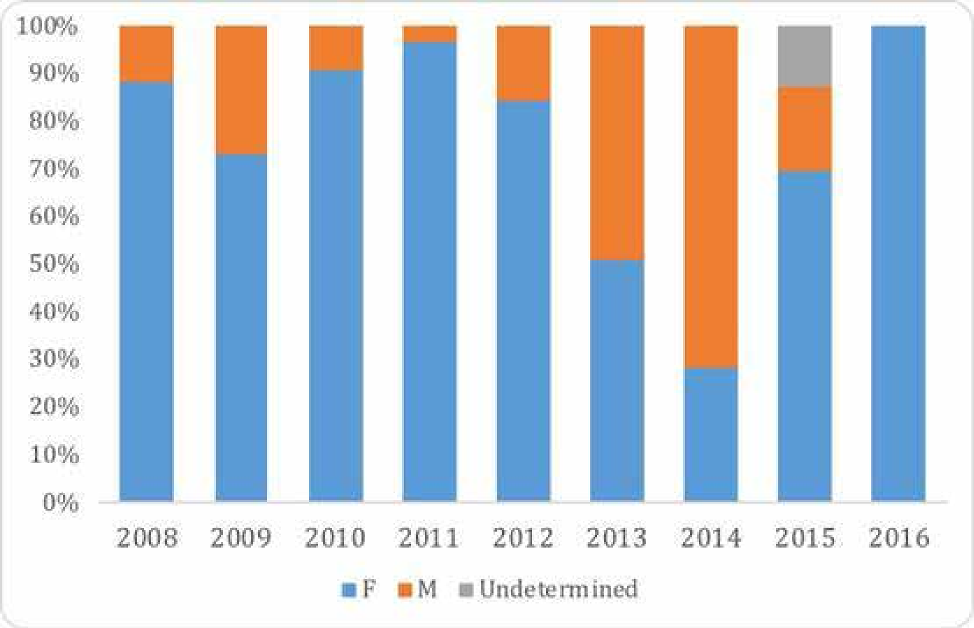


Figure 1. Sex ratios of hatchlings (as determined by histology of gonads from dead hatchlings) from Rushikulya on the east coast of Odisha

There are significant nesting beaches for leatherback turtles (Dermochelys coriacea) in India on Great and Little Nicobar Islands, and Little Andaman Island. This turtle was tagged with a satellite transmitter at West Bay, Little Andaman Island. Leatherbacks that nest on these beaches migrate southeast towards Western Australia, as well as southwest to the Mozambique and Madagascar (Photo: Kartik Shanker)

Other reptiles such as crocodiles, freshwater turtles and some lizards are also known to exhibit TSD (Sarre et al. 2004). In crocodiles, cooler and hotter incubation temperatures produce females, and intermediate temperatures produce males (Lang and Andrews 1994). 1994). Masculinisation of populations could have even more immediate impacts on population viability. Little is known about the mechanisms of sex determination in geckos and skinks which can show both genetic sex determination and TSD. There are a large number of endemic lizards in India with restricted distributions, which could be affected by the impact of changing temperature regimes on sex ratios, physiology and behaviour.

In summary, climate change can affect the future of sea turtle populations by its impacts on sex ratios, hatching success and habitat/availability of food (Fuentes et al. 2013). While climate mitigation may be required at a global scale, there are conservation and management approaches that can increase the resilience of these species and their habitats at a local scale.

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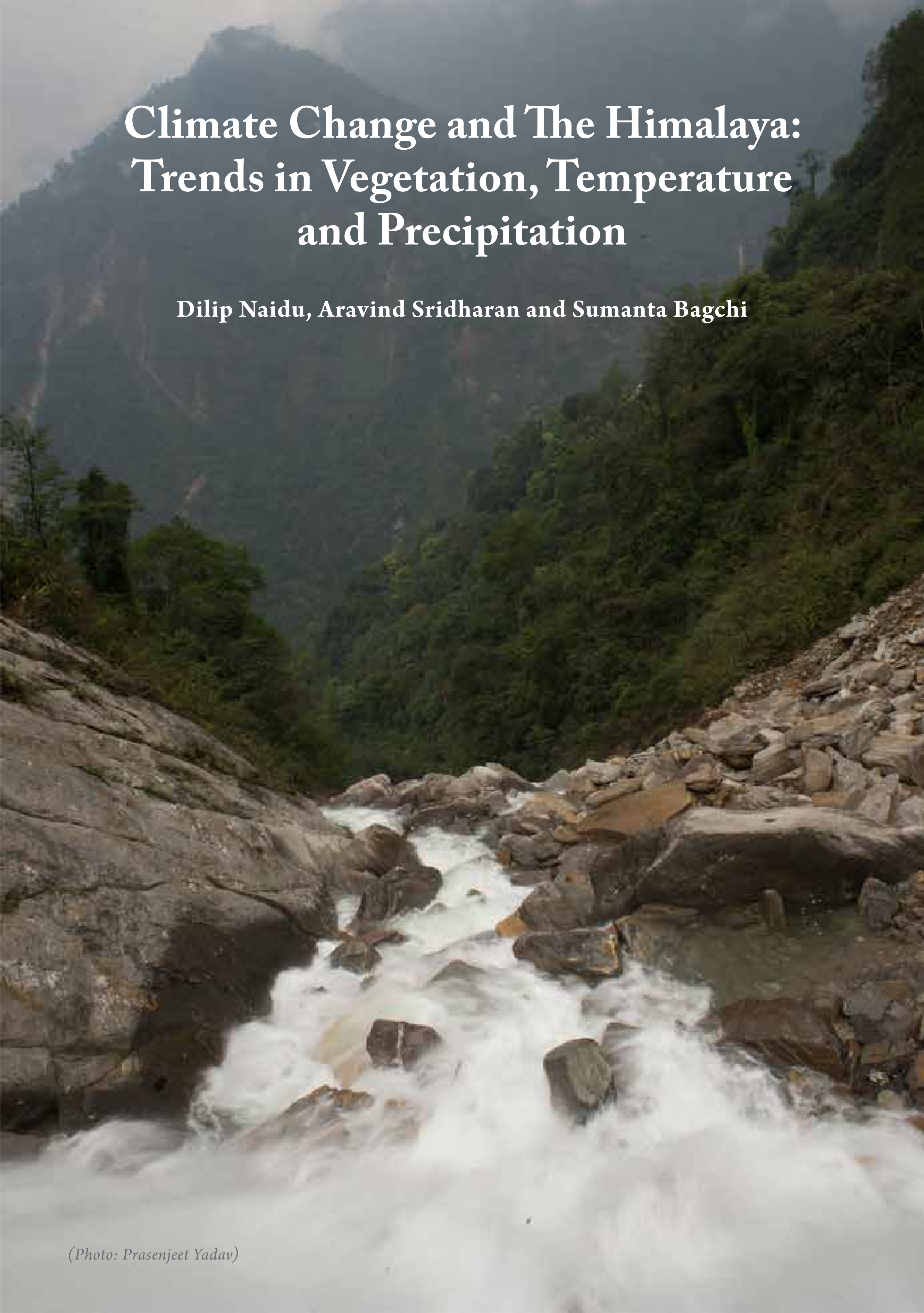
Climate Change and The Himalaya: Trends in Vegetation, Temperature and Precipitation

Dilip Naidu, Aravind Sridharan and Sumanta Bagchi



(Photo: Prasenjeet Yadav)

GLOBAL CLIMATE CHANGE

Global mean average temperature has increased steadily in the industrial era, and the planet is expected to be 2°C warmer by 2100, compared to the pre-industrial baseline (IPCC 2013). The past century has seen steady accumulation of carbon dioxide (CO_2) in the atmosphere, driven by a variety of human activities, and resultant radiative forcing towards a stronger greenhouse effect. Dynamic change in the climatic systems has led to uncertainty in understanding the alterations to biogeochemical cycles and their consequences (Finzi et al. 2011). Although anthropogenic factors act locally in different parts of the world, they can have wide-ranging implications at a global scale. These changes are especially relevant to the Himalayan region (IPCC 2001; Tse-ring et al. 2010; Bhattacharjee et al. 2017).

CLIMATE CHANGE IMPACTS IN THE HIMALAYA

The Himalaya serves as a primary water source for over 1 billion people in the Indian subcontinent. Climate change can affect the hydrological cycle and modify precipitation patterns over the Himalaya, which can intensify precipitation events, droughts, floods, landslides and avalanches (IPCC 2001). Subsequently, changes in water balance can lead to multifold crises from a shortage of drinking water to affecting irrigation and food security (Immerzeel et al. 2010). As major rivers of the subcontinent originate from this region, the need for mitigation efforts is extremely high. The ability of climate to change quickly, in a matter of decades, can modify the vegetation dynamics and affect the vast landscape.

Rapid rise in mean average temperature in the Himalaya compared to the global average (Bhutiyani et al. 2008), together with shift in precipitation patterns can help invasive plant species to flourish and drive endemic species to extinction (Grabherr et al. 1994; Pauchard et al. 2009; Telwala et al. 2013; Lamsal et al. 2018). Approximately 40% of forest cover is predicted to decline in the Himalayan region during the 21st century, with higher decline in the western Himalaya compared to the east (Pandit et al. 2007). Such landscape level transformations in ecosystem structure can impact human livelihoods (Manish et al. 2016). High reliance on ecosystem services in the form of agriculture, medicinal plants, and livestock products makes local inhabitants highly vulnerable (Sharma et al. 2009; Pandit et al. 2014).

SNOWPACK AND HYDROLOGY IN THE HIMALAYA

Glaciers play a pivotal role in controlling climate dynamics in the Himalayan region. They help regulate albedo and serve as the water source of major rivers. Changing climatic conditions can modify the hydrology of the landscape to great extents. Models and empirical measurements from various studies have found a general decline in most Himalayan glaciers, similar to glaciers elsewhere. The Space Applications Centre (SAC) of the Indian Space Research Organisation (ISRO), Ahmedabad, carried out a study of 2018 glaciers, based on IRS LISS III data with 23.5 m spatial resolution. This study was carried out to find changes in the extent of Himalayan glaciers in Karakoram, Himachal, Zanskar, Uttarakhand, Nepal and Sikkim regions, using satellite data from 2000-2001 to 2010-2011. In its report, SAC-ISRO observed that 1752 glaciers showed no change, 248 showed retreat and only 18 showed advancement (Bahuguna et al. 2014). Other studies have suggested that most Himalayan glaciers have thinned over the past few decades (up to -0.26±0.06 m/yr) and lost mass (Bolch et al. 2012; Kääb et al. 2012). Smaller glaciers are predicted to recede at a faster rate compared to the larger glaciers (Bajracharya et al. 2007). Such rapid recession in glaciers can lead to decline in discharge in the upcoming decades (Bhutiyani et al. 2008), which can impact large human populations in the Indus, Ganges, and Brahmaputra catchments.

(Photo: Urbashi Pradhan)

Although temperature and precipitation determine glacial dynamics globally, glacier size, elevation, aspect, altitude, and debris cover can impact the mass balance and survival of glaciers on a regional scale (Fujita and Nuimura 2011). Presence of debris has shown contrasting results on glacial melt, thus making it hard to distinguish the effect of 'dirty' glaciers from 'clean' glaciers (Kääb et al. 2012; Racoviteanu et al. 2014). Highly localised effects such as area covered by debris and its association with lakes determine the glacier transport capacity, leading to uncertainties in estimating net mass balance (Basnett et al. 2013). The lack of high-resolution data coupled with complex dynamics has been the main reason for the relatively incomplete understanding of glacial dynamics. This necessitates the need for robust remote sensing methods and on-site measurements (Bolch et al. 2012; Chaturvedi et al. 2014).

TEMPERATURE AND PRECIPITATION TRENDS IN THE HIMALAYA

Impacts of warming in the Himalayan region is evident from a plethora of studies. One such study for the period 1984-2007 in the Western Himalaya reported seasonal increase in temperature with approximately 2°C, 2.8°C and 1°C rise in mean, maximum, and minimum temperatures, respectively (Shekhar et al. 2010). Under different temperature scenarios (T+1, T+2, T+3 where T is the current temperature), evaporation is reported to increase, and snow cover area will reduce (Singh and Bengtsson 2005). For the given rise in temperature, snowmelt decreased in the snow-fed basins (11-23%) and increased in the glaciated basins (16-50%), whereas the rest of the basins showed no trend.

We reviewed temperature records in the Himalaya and found contrasting trends in Western and Eastern Himalaya (Climate Research Unit, CRU data, with 0.5° spatial resolution, or 55 km at the equator). During the period 2001-2015, winter temperatures in Western Himalaya decreased mostly in the southern parts (Figure 1). But, the temperature during the growing season has increased. Eastern Himalaya, however, showed warming signs throughout the year, which coincides with trends from other reports (Kapnick et al. 2014).

Distribution of annual precipitation in the Himalaya varies widely from west to east. Temperature sensitivities of different regions distinguish the partitions of precipitation into rain and snow. Western Himalaya is heavily influenced by winter snowfall, whereas the east primarily receives rains from the south-

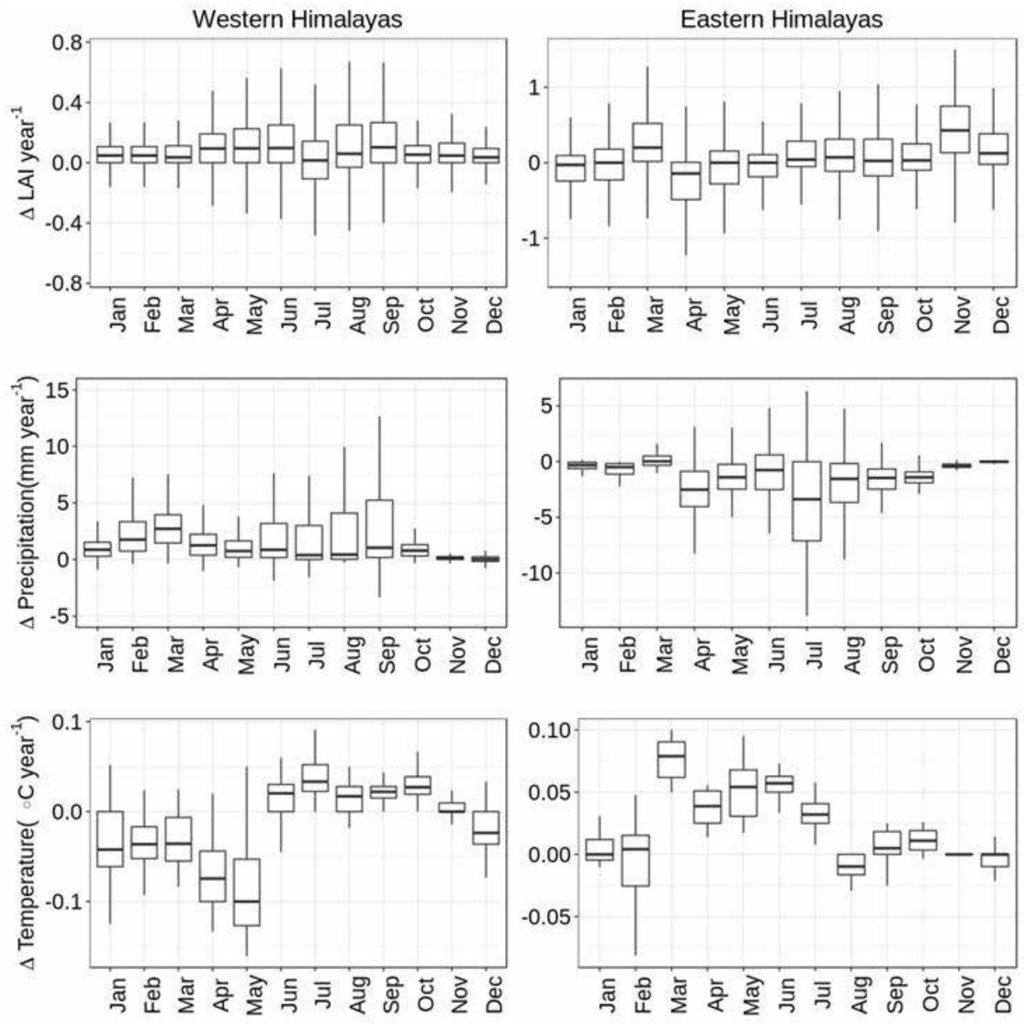


Figure 1. Changes in Leaf Area Index (LAI), temperature and precipitation in the Eastern and Western Himalaya from 2001-2015. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

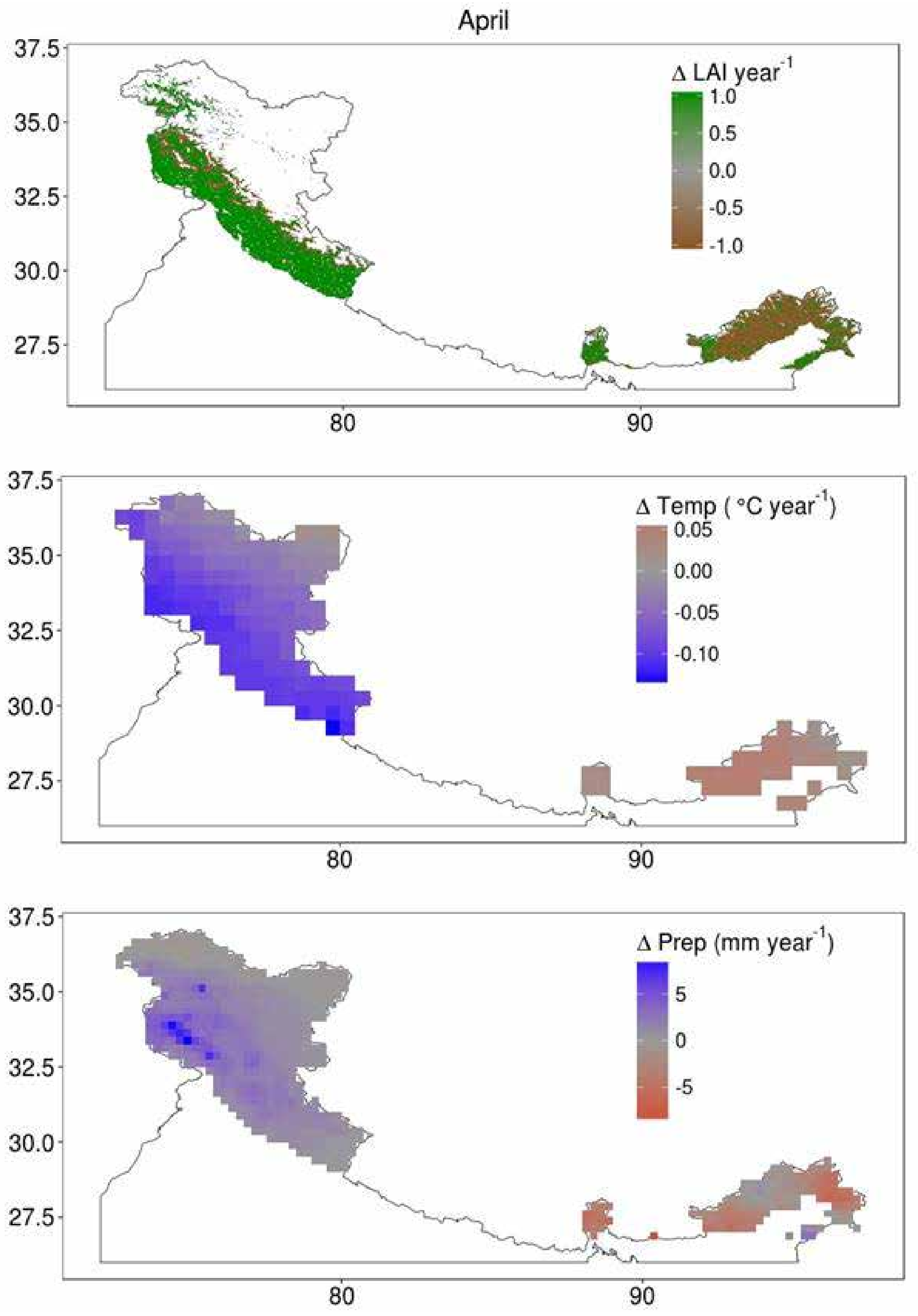


Figure 2. Trends in Leaf Area Index (LAI), temperature and precipitation in Himalayan region from 2001-2015 for the month of April. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

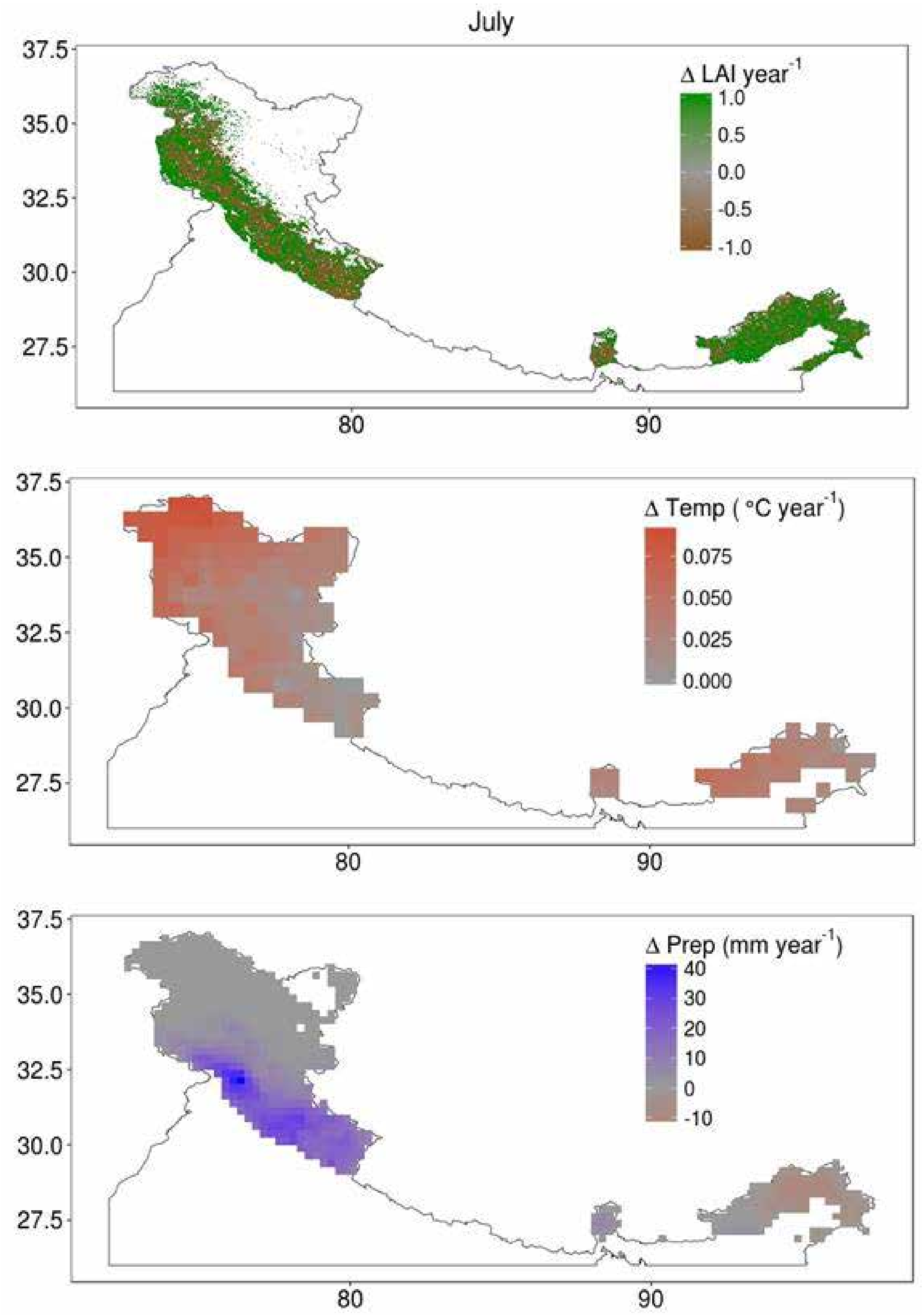


Figure 3. Trends in Leaf Area Index (LAI), temperature and precipitation in Himalayan region from 2001-2015 for the month of July. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

Cold desert in the Himalaya (Photo: Vikram Sathyanathan)

west Indian monsoon (Kapnick et al. 2014). Studies have reported that annual precipitation has changed in the past century. One of the causes for decrease in snowfall has been attributed to increase in winter air temperatures, which has been linked to anthropogenic forcing (Bhutiyani et al. 2007, 2010).

We reviewed historical precipitation records during 2001-2015 (Climate Hazards Group Infra-Red Precipitation with Station, CHIRPS, with 0.25° spatial resolution). The results show that Eastern Himalaya has undergone drying with a rise in temperature and decrease in the monsoon showers (Figure 2). Western Himalaya has experienced an increase in snowfall in the winter season as temperatures have reduced, whereas the monsoon rainfall showed a slight increase (Figure 3). Increase in the winter temperatures coupled with glacial melting can affect the length of the winter season, with consequences for ecology and hydrology.

Climate change can modify precipitation patterns across the region affecting spring discharge in the high mountains. This can impact water availability for rural populations (Tambe et al. 2012; Pandit et al. 2014). Positive correlation has been noticed with global warming and frequency of extreme events, which could affect the number of snowfall days (Shekhar et al. 2010). Diminishing albedo due to rise in temperature and glacial melting can lend positive feedback to radiative forcing, and has been linked with higher sensitivity in maximum precipitation and glacier melting at the lower latitudes (Fujita 2008). In the Eastern Himalaya, Sikkim has seen a rise in the mean annual air temperature and a decline in winter precipitation. As the region is highly sensitive to temperature and dominated by monsoon, a reduction in snowfall is expected (Basnett et al. 2013). Variation in temperature and precipitation can influence the snowmelt as well as run-off during the summer monsoon, both of which can influence the likelihood of flash-floods in the Western Himalaya (Bhutiyani et al. 2008).

Fluctuations in the length of the winter and growth season together with biotic factors are thought to be responsible for upward treeline shifts (Forrest et al. 2012). This process is expected to accelerate with increasing temperature under different climate change scenarios (Yadava et al. 2017). Warming across arid regions of the Himalaya has been linked with desertification by increasing snowmelt and decreasing plant production, which in turn affects livestock or results in direct reduction in grasslands (Aryal et al. 2014). However, these patterns have been found to be very heterogeneous, and vary across space and seasons (Murthy and Bagchi 2018). Snow-free period has also been shown to modify phenological patterns from observatory data (Kudo 1991). Further, increase in livestock pressure can alter species composition and mediate shifts in ecosystems (Nautiyal et al. 2004; Bagchi and Ritchie 2010). Such disparity in predictions on biodiversity's ability to cope with climate change has made managerial efforts harder to implement.

Changes in Seasonality of Vegetation Growth

Diverse taxa including plants, insects, birds, reptiles and mammals are all prone to impacts of climate change (Parmesan and Yohe 2003). Although biodiversity and vegetation distribution change have been attributed to climate change, the interactions between multiple causal factors still remain uncertain (Kelly and Goulden 2008; Pereira et al. 2010). Phenological studies, including citizen science initiatives (e.g., SeasonWatch, http://www.seasonwatch.in), and other studies have encountered bidirectional changes (i.e., delay or advance) in flowering in response to winter temperatures (Hart et al. 2014). Start of season (onset of vegetation growth) and senescence (end of season) determine the photoactive period in terrestrial ecosystems. Winter temperatures, photoperiod, and temperature are the three major drivers that control the phenology of species (Rathcke and Lacey 1985; Körner and Basler 2010; Cook et al. 2012). Global warming can cause shifts in plant phenology by altering these factors, and in turn affect biogeochemical cycles, disrupting flow patterns. Previous research has highlighted modifications in the start and end of seasons as a result of precipitation and temperature patterns primarily at higher altitudes (Yu et al. 2010; Shrestha et al. 2012; Shen et al. 2015). In such situations, plants sensitive to the onset of growth seasons and temperature are likely to outcompete species which are obstinate to climatic changes (Gottfried et al. 1999; Ashcroft et al. 2009; Körner and Basler 2010; Cleland et al. 2012; Wolkovich et al. 2013). In-depth examination of phenological sensitivity of plants can help conserve endemic and highly endangered species.

One of the methods to understand the phenology shifts and vegetation dynamics is via remotely sensed data from satellites (Murthy and Bagchi 2018). Satellite-derived indices such as Normalized Difference Vegetation Index (NDVI) and Leaf Area Index (LAI) reflect ecosystem dynamics based on vegetation cover. Rising variability in climatic conditions and land-use patterns have caused greening (increasing vegetation) and browning (decreasing vegetation) at different parts of the globe, and these are directly linked to the status of carbon and hydrological cycles (Krishnaswamy et al. 2009). Looking at changes in vegetation cover in these regions helps focus on areas that are important for conservation.

We reviewed LAI data from moderate resolution imaging spectroradiometer (MODIS data at 1 km resolution at the equator) for the period 2001-2015. Western Himalaya shows a general positive trend, with increase in the growing season caused by increase in temperature and a longer photoactive period (Figure 4). Eastern Himalaya has more or less remained unchanged, except for a decrease during the

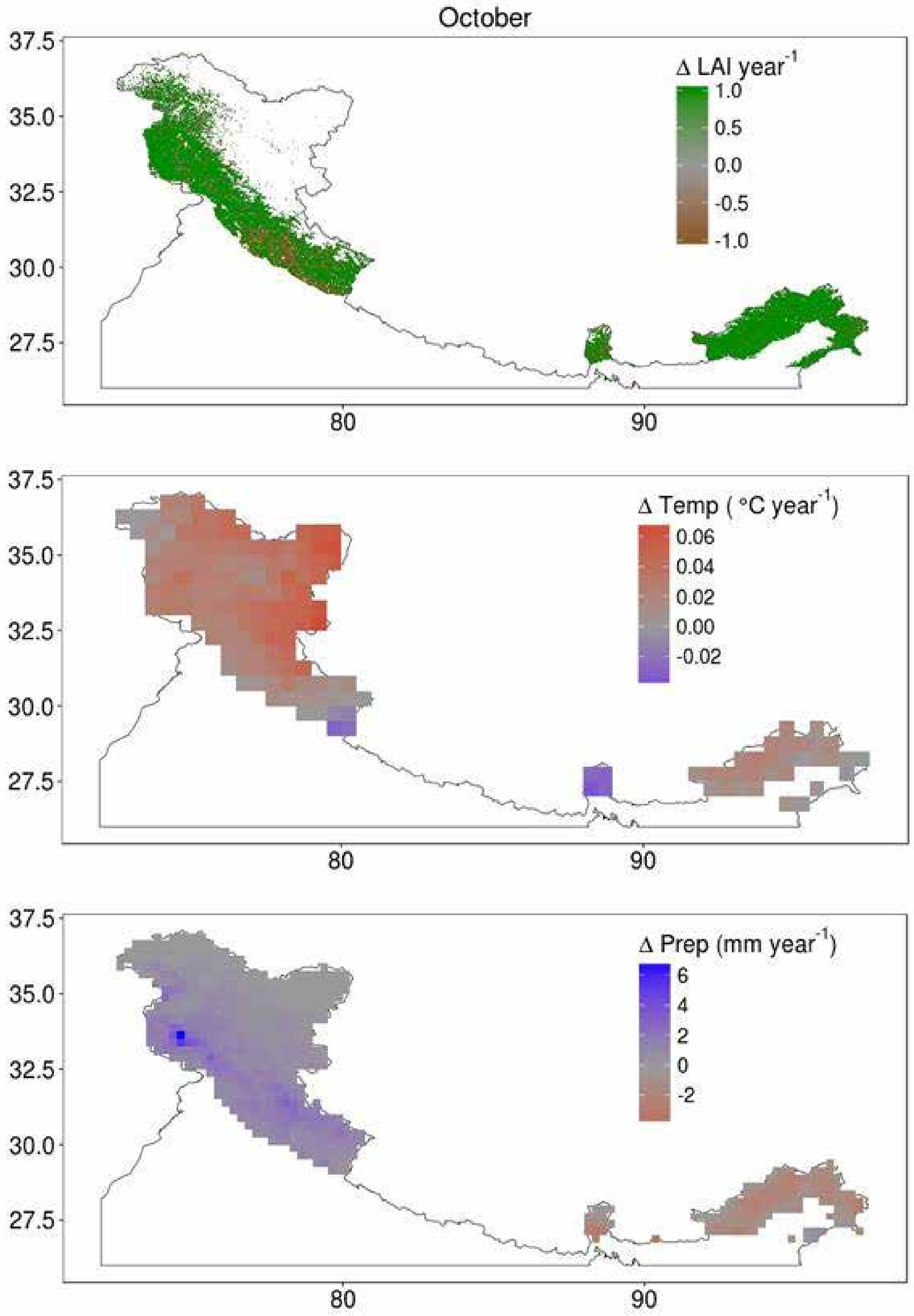


Figure 4. Trends in Leaf Area Index (LAI), temperature and precipitation in Himalayan region from 2001-2015 for the month of October. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

start and an increase at the end of the growth season. This can possibly be an indication of decrease in the length of the winter season, represented by decrease in vegetation cover (browning) in this region (Figure 2).

Outlook for Climate Mitigation

Species composition, local warming, land-use and other intrinsic factors play a major role in vegetation dynamics, which in turn influence how management decisions are taken for an ecosystem (Baker and Moseley 2007). Alpine and subalpine species are extremely sensitive to climate change and show long recovery time from disturbances (Bawa et al. 2010). Afforestation of abandoned agricultural lands together with the network of biosphere reserves and protected areas, where ecosystems can adapt or mitigate the effect of climate change with reduced human footprint, can help sustain montane vegetation (Beniston 2003).

Adaptation to climate change varies at different levels, starting from local communities (by collaborating with villagers), to urban and rural regions (where effective policies can be implemented), and further towards transboundary efforts (where different countries combine their conservation ideologies) (Xu et al. 2009; Singh et al. 2011). Cooperation between India and China can boost conservation efforts across the Himalayan region. Adaptability and flexibility for the local populations toward conservation has been a major drawback. Lack of motivation and clear incentives, leading to reduced support from local populations, creates complexity in management (Bawa and Seidler 2015). Some simple mitigation efforts include identification of vulnerable areas, improvement in waste management and use of low-carbon sources of energy (Bhutiyani 2018). Past and ongoing research has highlighted the necessity of understanding the dynamics of the Himalayan region, to help make management decisions at the earliest, and protect the high mountains of Asia.

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Rhododendron flowering in the subalpine region: Kyongnosla (Photo: Shweta Basnett)

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CLIMATE CHANGE AND BIRDS OF SHOLA SKY ISLANDS

V.V. ROBIN

The rufous-bellied sholakili (Sholicola major) *in the Nilgiri Hills, north of the Palghat Gap, has been isolated from its sister species for about 4.5 million years, possibly due to paleoclimate change (Photo: Prasenjeet Yadav)*

Climate change is known to impact mountains and the communities they host. Although the impacts of the recent anthropogenic climate change are progressing at an alarming rate, paleoclimate, over a long period, has also had a historic role in the creation of the rich biodiversity of mountains.

During the natural paleoclimatic fluctuations that occur over hundreds of thousands of years, the Indian subcontinent went through cycles of dry and wet periods. These climatic fluctuations resulted in the expansion and contraction of forests and grasslands across much of the subcontinent.

The highest elevations of the Western Ghats have some of the most spectacular landscapes in southern India. These mountaintops (above 1400 m) have unique habitats called shola, also known as tropical montane cloud forests. Series of such mountains in this chain implies that the habitat is naturally fragmented across these mountains, forming what are now called the 'sky islands'. Each wet/cold mountaintop island is isolated from others by dry/warm climate and related habitats. Tropical coastal mountaintops like these shola sky islands are known to host climatically stable habitats on mountains. Here, on the highest mountains, the forests are relict habitats that are thought to have survived paleoclimatic fluctuations, perhaps driven by cloud-driven climate patterns. These cloud forests serve as refugia for forests and forest-dependent species while the climates at lower elevations alternate between wet and dry, resulting in rapid changes between wet forests and dry habitats. As the climate across the peninsula becomes dry, forests contract upward and become extremely isolated, with grasslands expanding from lower elevations. In the long term, such events lead to speciation and diversification. As the climate cools and habitats associated with such climates spread to lower elevations – bringing habitats from adjacent mountains in contact with each other – the colonization of organisms between the previously disconnected mountaintops is facilitated. Over historical time, several such cycles are thought to have occurred, resulting in a high diversification rate and biodiversity in such mountain areas.

Despite such fluctuations, species living on the tops of these mountains have survived in the refugia through severe climatic events like ice ages. The newly described Western Ghats bird genus *Sholicola* (previously shortwings) or sholakili have lived on the shola sky island mountains for millions of years - about nine million years (Robin et al. 2017). They had diverged and radiated across different sky islands as early as five million years ago, across the Palghat Gap. Research shows that older, ancient lineages of various organisms like frogs, snakes, mammals and birds are also found on such mountaintops. This is true not only in India, but also on the tropical coastal mountains of Indonesia, Africa, and South America. Paleoclimatic fluctuations over a long timescale (millions of years) interacting with topography can thus have a positive effect on biodiversity.

Anthropogenic climate change is thought to occur over and beyond paleoclimatic fluctuations, and is known to be an order of magnitude faster in pace, making it difficult for many species to adapt or cope. It is known to impact bird communities in various ways, with one of the most common being upslope movement of lower elevation birds. By this process, species whose ranges are normally at lower latitudes move northwards, while montane species at low elevations move to higher altitudes on mountains. Considering the rapid pace of anthropogenic climate change, species that move rapidly are usually generalists or those that have broader niches. However, this shift in their ranges could increase competition and may further reduce the range of specialist birds on mountaintops.

Such a phenomenon has been recorded in various parts of the globe, and poses

Sky islands of the Western Ghats (Photo: Prasenjeet Yadav) increased extinction threats for high-elevation specialists. Yet, there are very few long-term datasets from India that have documented such changes. Dr Salim Ali, the famous ornithologist, had conducted meticulously documented surveys of specific regions. His work in the Western Ghats – the Travancore and Cochin surveys of 1933 – involved making note of the birds documented at each site. About 75 years later, in 2009, a team of researchers (Sashikumar et al. 2011), with the support of the Kerala Forest Department decided to retrace Salim Ali's trail and document birds within the same week of the original surveys (summarised in Sashikumar et al. (2014)). Similar to the global pattern, they also recorded several upslope movements of low-elevation generalists like the red-whiskered bulbul (*Pycnonotus cafer*). Drier habitat birds like the peafowl (*Pavo cristatus*) and human-associated species like the house swift (*Apus affinis*) and black kite (*Milvus migrans*) were also observed to have increased.

*The white-bellied sholakili (*Sholicola albiventris*) in the Anamalai and Palani Hills is an endemic bird that has been placed in a newly described genus signifying the shola sky islands (Photo: Prasenjeet Yadav)*

Often, patterns from climate change interact, and can be exacerbated by landscape change. In the Western Ghats mountaintops, parts of the landscape have changed drastically even in the last half-century (Arasumani et al. 2018). Sashikumar and team noted the local extinction of species including vultures from their resurveys. It is difficult to tease out direct human impacts in such cases, though interactions are documented across the globe.

There are no other long-term studies on a mountain gradient to infer the effects of climate change on birds. Generating such baseline data and time-series sampling is one of the urgent requirements to document impacts on biodiversity.

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Climate Change and Aquatic Biodiversity

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*Gharial (*Gavialis gangeticus*) female, Chambal River, Uttar Pradesh (Photo: Charles J. Sharp; Wikimedia Commons)*

INTRODUCTION

Aquatic (freshwater) biodiversity in India includes plants and animals found in wetlands, streams, rivers, estuaries and riparian fringes. Due to the large-scale appropriation of water and degradation of these ecosystems (due to pollution and over-extraction), aquatic biodiversity is one of the most threatened components of biodiversity in India. Past, ongoing and planned large-scale transformations of our wetlands, streams and rivers are the biggest threats to aquatic biodiversity (Dudgeon 2000; Bandyopadhyay and Perveen 2004; Vörösmarty et al. 2010; Grant et al. 2012; Gopal 2013; Jumani et al. 2018), and these will be exacerbated by climate change (Immerzeel et al. 2010). These transformations include small hydropower projects and inter-basin transfers of headwater streams, introduction of invasive species, interlinking of rivers (and its consequences for hydrology), destruction of habitats, pollution and invasive species transfer, besides the looming threat of the National Waterways, which involves changes in channel geometry, destruction of habitat and water quality through large-scale dredging, and water and noise pollution from vessel traffic (Kelkar 2016; Dharmadhikary and Sandbhor 2017). Climate change through warming and changes in rainfall regimes will impact streams and rivers in two distinct ways. Climate warming may change the microclimatic environment, especially in terms of heat stress for many freshwater organisms, and also impact the temperature of rivers, thus causing shifts in ecosystem productivity and species response. In the case of reptiles such as crocodilians, this could mean a change in the sex ratio of hatchlings.

Climate change impacts on the rapid retreat of Himalayan glaciers, increased temperature and variability in precipitation, as well as the frequency of extreme events are already impacting aquatic ecosystems from headwaters to deltas. However, the actual threat to wetlands in this region arises from the extensive hydrological alterations being caused by storage, abstraction and diversion of river flows for agriculture, industry and hydropower; climate change could further add to their degradation. In the world's largest mangrove ecosystem, the Sundarbans, this has already led to changes in the salinity regime, and shifts in species composition – and this will be further enhanced under sea level rise (Raha et al. 2012). Overall, large-scale transformations (including inter-basin transfers and waterways) are likely to reduce species richness of specialist species, increase abundance of invasive and generalist species, transform the distinctive biogeographically and geologically established patterns of aquatic biodiversity, and possibly cause the extinction of species such as the Gangetic and Indus river dolphins (Grant et al. 2012; Kelkar 2016). However, changes in meltwater contributions could severely impact the Indus and Brahmaputra rivers and the associated aquatic ecosystems in the long term (Gosain et al. 2006; Immerzeel et al. 2010).

CLIMATE CHANGE AND AQUATIC ECOSYSTEMS IN INDIA

The predicted impacts of climate change on freshwater ecosystems have important convergences, as well as inconsistencies and uncertainties. Across river basins, we can find consistent predictions of increased water and air temperature, but widely varying precipitation and run-off responses (e.g. Webb and Nobilis 2007; Kingston et al. 2011). Greater frequencies of summer and winter rainfall extremes, short-term increases in flooding followed by long droughts, plus decreases in dry-season river flows, are some of the consistent model projections

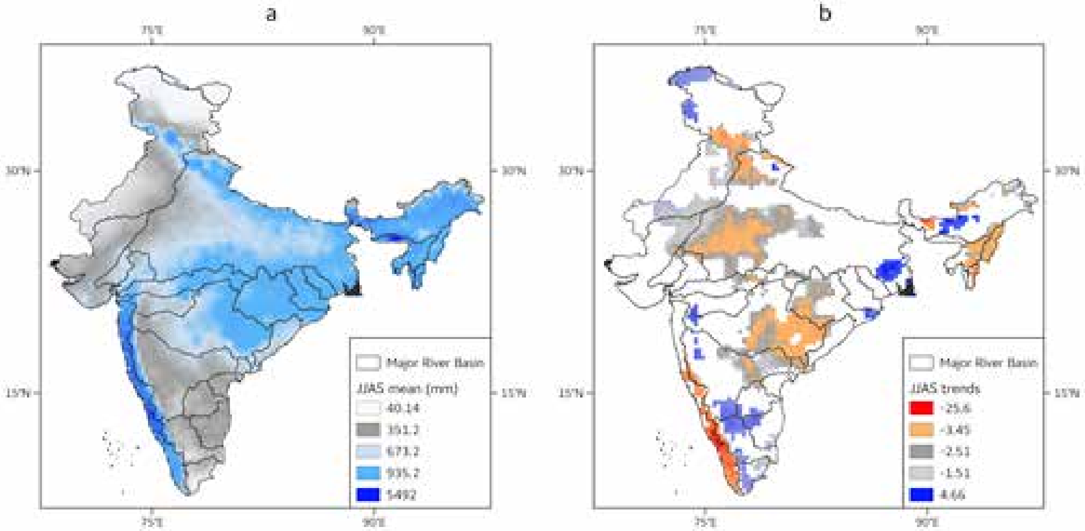


Figure 1. Historical analysis of southwest monsoon using high resolution Aphrodite data. a) long-term average (1951-2007) rainfall across India shows high rainfall regions in the Western Ghats and north-east India. b) Observed non-parametric trends in SW monsoon totals show large-scale decline in the Western Ghats and central Indian river basins. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

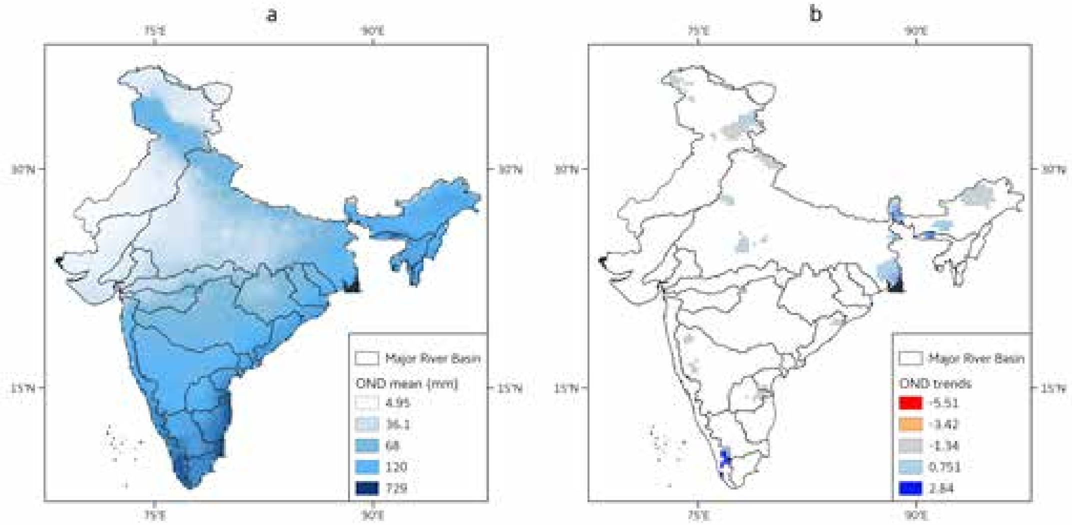


Figure 2. Historical analysis of northeast monsoon using high resolution Aphrodite data. a) Long-term average (1951-2007) rainfall across India shows high rainfall regions in the southern Western Ghats and along the east coast of India. b) Observed non-parametric trends shows isolated locations which show an increase in NE monsoon totals. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

for river systems worldwide (van Vliet et al. 2013; Dallas and Rivers-Moore 2014). Predicted increases in river CO_2 concentrations and the new addition of carbon into freshwaters might be balanced by temperature-driven increases in silicate dissolution and CO_2 absorption into river water (through higher sediment weathering and deposition rates), and such biogeochemical feedbacks can impact river-floodplain productivity (Hamilton 2010). Sea level rises and ingress into estuaries are predicted to cause serious levels of river salinisation in the near future (e.g. Dasgupta et al. 2015).

Yet there is significant variability in our understanding of the exact pathways of change. Increased snowmelt and glacial retreat are being recorded globally, but their effects on river discharge in the plains can be quite variable. For example, the eastern Amazon might witness decreased, while the western sub-basin would witness increased discharges and flood inundation periods, in response to future reduction in Andes snowmelt (Sorribas et al. 2016). Inputs to the larger part of the basin are dominated by lowland sources; as a result, other studies expect no major influence of Andean snowmelt on the Amazon plains of Brazil (Hamilton 2010). In contrast, the accelerated rates of snowmelt in the Himalayas and the Qinghai-Tibetan Plateau are likely contributing to increased springtime dry season flows, and affecting the onset of flooding in the Gangetic plains (Xu et al. 2009; Anand et al. 2018). In the Indus-Ganga-Brahmaputra basins, this may also have increased flooding risk (Nepal and Shrestha 2015).

The South Asian summer monsoon is the vital force that sustains millions of people, and several endangered species in rivers of the Indian subcontinent (Dudgeon 2000), but climate predictions are still variable due to its complex nature. Future rainfall projections reveal spatially non-uniform changes, with increase in some parts of the country and decrease in others (Salvi et al. 2013). Furthermore, as predicted by the physics of a warmer atmosphere, the frequency of high-intensity rains is already increasing in parts of India (Figures 1, 2 and 3) since the 1950s, and is likely to emerge as a major change in monsoonal regimes over the next few decades (Goswami et al. 2006).

How are river flow regimes likely to change in India? This is an assessment with high uncertainty due to the uncertainty associated with the precipitation projections and other sources of uncertainty as well. Under the A1B development and emission scenario, reductions in river flow were found for most of India while increases were mostly predicted under the A2 scenario (Falloon and Betts 2006). Changes in river flow are likely to increase in severity with time. Significant changes in the seasonality of river flow could also occur, such as earlier peaks in spring run-off in the Himalaya due to earlier snowmelt. Climate change is likely to increase the occurrence of both high and low flows, although the occurrence of high flows could be dominant.

There are substantial regional uncertainties with respect to hydrological impacts at basin scales due to different climate models producing different outcomes. Overall hydrological impacts of future climate generally point towards wetter conditions on average, with increased mean river flows, longer heavy rainfall events, and a few projections suggesting a doubling of flows in the Ganges at 2°C global warming (Betts et al. 2018). The modelling results from another study (Zheng et al. 2018) indicate that future run-off will increase throughout most of India (Figure 4) except in the far north-east and far north-west. The median projection shows increases of 20–30% in

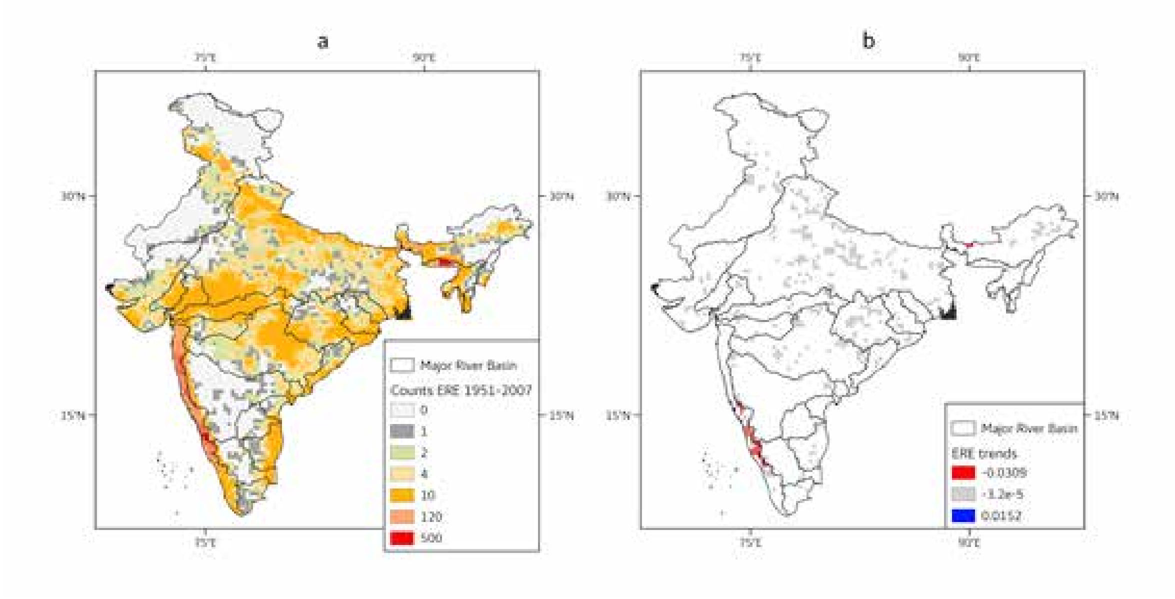


Figure 3. Historical analysis of extreme rain event (ERE): rain event >=100mm/day using high resolution Aphrodite data. a) Long-term map (1951-2007) of total number of EREs across India indicates areas in Western Ghats and northeast India record the highest number of events when compared to the rest of India. b) Observed non-parametric trends indicate major declines in EREs in the Western Ghats. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

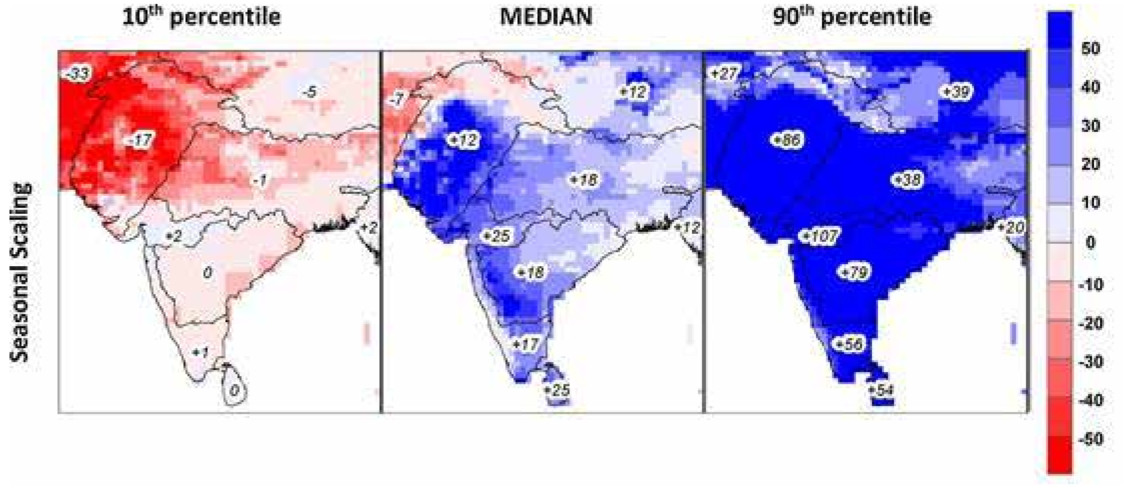


Figure 4. "Future climate and runoff projections across South Asia from CMIP5 global climate models and hydrological modelling" by Zheng et al. (2018), used under CC by ATREE. Cropped from original. The future run-off projections from the seasonal scaling is wetter than those from the annual scaling, showing 2–4% greater increase in future mean annual run-off. This is attributed to the proportionally higher projection of precipitation increase in the summer monsoon (JJAS), when higher run-off occurs, compared to winter. The seasonal scaling treatment, therefore, enhances the summer monsoon run-off and subsequently the annual run-off compared to the annual scaling treatment. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

mean annual run-off in the Indian sub-continent for 2046–2075 relative to 1976–2005. In general, the variability in run-off projections from different hydroclimatic scaling methods is small relative to the large uncertainty in precipitation projections from the GCMs.

Recent work has brought out the importance of rapid subsurface pathways that can transfer large quantities of rain in the headwater catchments in the Western Ghats, a hotspot for endemic fish, to streams. This subsurface watershed residence time decreases non-linearly as rain intensity rises. Projected increases in rainstorm intensity under ongoing climate change would then result in a greater likelihood of river floods in subsurface-dominated watersheds (such as in the Western Ghats) than is currently simulated by catchment models (Chappell et al. 2017). This is likely to make river environments particularly flashy, and may be detrimental to many aquatic plants and animals depending on their traits, and also likely to change stream and river flows with more flashy behaviour. In combination with land-use, this may result in less recharge to ground-water and thus reduced base-flows in rivers and streams. Though the overall predictability of its complex dynamics remains weak, extreme rainfall events are increasingly evident, apart from appearing trends of reduction in total annual/seasonal rainfall over the last 5-6 decades (Turner and Annamalai 2012). In South Asia, weakening summer monsoon and increasing spatial extremes (especially in central India) are significant predictions (Krishnan et al. 2016) in this regard. Weakening monsoons are also probably linked to local unseasonal precipitation, with irrigation as a major reason (Paul et al. 2016). This is a good example to illustrate how climate adaptation of many riverine species can be impaired by synergistic effects of river regulation in plains (for diverting water to irrigation) and its returning impact on the monsoon itself, with obvious consequences for flooding regimes and riverine biota.

Climate change predictions indicate that the annual mean temperature for India is likely to increase by 1.7-2.02°C by the 2030s under different RCP scenarios, and by about 2-4.8°C by 2080s, relative to the pre-industrial baseline. Generally, the northern part of the country is projected to experience higher warming compared to the southern part (Chaturvedi et al. 2012). Kothawale and Rupa Kumar (2005) have shown significant warming in both maximum (0.20°C/10yr) and minimum temperatures (0.21°C/10yr) during the last 5 decades (Figure 5). Chaturvedi et al. (2012) state that under the business-as-usual (between RCP6.0 and RCP8.5) scenario, mean warming in India is likely to be in the range 1.7-2°C by the 2030s and 3.3-4.8°C by the 2080s relative to pre-industrial times.

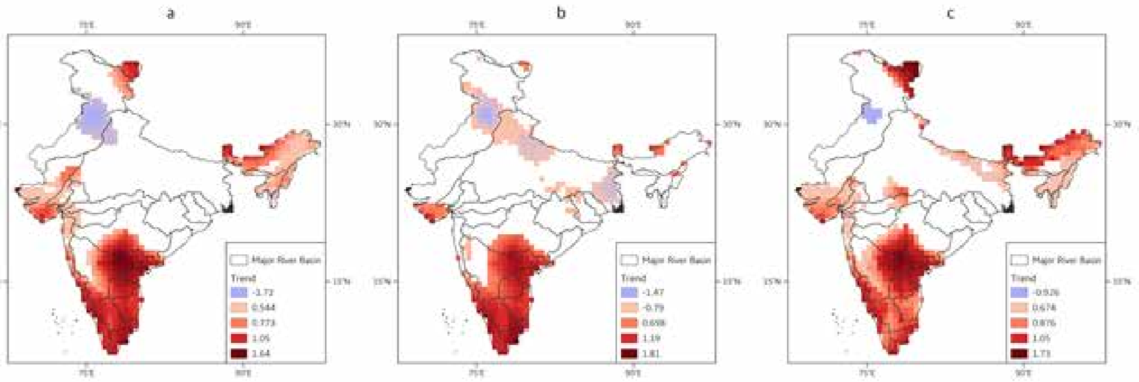


Figure 5. Historical (1951-2007) analysis of observed temperature using CRU dataset. a) Trend in long term annual mean temperature shows increase in temperature in southern, western and north-east India. b) and c) show the observed trend in annual maximum and minimum temperatures respectively. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

Model performance with respect to historically observed trends in temperature is generally good, except for some pockets in peninsular India and a major swath in the Gangetic plains (at the foot of the Himalayas) that were much warmer in the models compared to observed temperatures. Temperature change under different RCP scenarios shows that in RCP2.6, by 2080, the majority of regions will experience a temperature rise of 2°C, with a minimum temperature rise of about 1.4°C and a maximum of about 2.8°C. The minimum temperature rise increases to 2°C in RCP4.5 and 3.4°C in RCP8.5.

Increasing trends are observed for river-water temperature, but this might also differ seasonally. The relative influence of snowmelt into surface flows (climate-driven) and groundwater contributions to base flows in the dry season (after man-made surface water diversions) might have similar effects on river temperature. Storey et al. (2003) showed that increasing contribution of groundwater to base flows can reduce stream temperatures. Groundwater reduced and water temperature increased in the warm and cool seasons respectively (Knouft and Ficklin 2017). At one level, groundwater depletion and declines in base flow due to abstraction might be augmented in the short term by increase in snowmelt fluxes due to climate warming. But such an effect will essentially be short-lived, based on the projected high melt-rates for glaciers. Arheimer et al. (2017) showed that it is much more important to manage hydropower regulation of rivers immediately – rather than worrying about future climate change effects. They demonstrate that hydropower and warming have similar effects – both reduce the magnitude of difference between dry- and wet-season flows (homogenisation). But the impacts of river regulation by hydropower (acting at shorter and faster timescales) are predicted to be much greater than landscape-level snowmelt changes. The effects of non-climatic drivers, therefore, should not be weighted low in light of climate change alarms (Diagram 1).

Hydrological and temperature impacts may be relatively predictable, but their effects on organismal biology and ecology are far more complex. Knouft and Ficklin (2017) review these complexities, and identify the role of multi-scale abiotic and biotic processes maintained and perturbed by man-made environmental changes on the one hand, and mediated by evolutionary histories and behavioural plasticity of species on the other. Their review re-emphasizes that great variability is to be expected in species and community responses to climate change. Broadly, responses can be grouped into three categories: climate uncertainty, extremes, and intensification of ecosystem processes can (1) indirectly alter environmental cues that freshwater species depend on for successful reproduction and migration/dispersal (e.g. seasonal temperature variations, flood-pulsed flow regimes), (2) directly affect species biology (e.g. thermal adaptation, sex determination, etc.), or (3) aggravate pre-existing man-made threats to many species, and probably even buffer some species from these threats, at different spatial and temporal scales, and across scales of biological organisation (individuals to communities) (Vescovi et al. 2009; Döll et al. 2009; Arthington et al. 2010; Woodward et al. 2010). They are likely to be specific to some life stages of larger vertebrates, vary with different life history traits, behavioural plasticity, and evolutionary/phylogenetic diversification of species.

IMPACTS OF CLIMATE CHANGE ON LARGE VERTEBRATE FAUNA OF RIVER ECOSYSTEMS

Exploring the impacts of climate change on riverine species of large vertebrates (especially reptiles, birds, and mammals) must start with the explicit recognition of two issues. The first relates to the fact that over the last two centuries, the ecology, biodiversity, and productivity of most 'riverscapes' across the world have been dramatically altered (and threatened) by human modifications such as dams and barrages (Nilsson et al. 2005; Dudgeon et al. 2006; Döll et al. 2009; Arthington et al. 2010; Vörösmarty et al. 2010; Liermann et al. 2012). This makes it difficult to disentangle the effects of climate change from the severe impacts that human interventions have already had on river ecosystems (Palmer et al. 2008; Vescovi et al. 2009).

The second is the consequent issue of limited information on complexities of 'natural' river ecosystem functioning, especially in human-modified tropical or subtropical environments (Tockner and Stanford 2002; Dudgeon et al. 2006; Arthington et al. 2010). In the wake of the transformations that rivers have witnessed, it is near impossible to identify ecological baselines of species diversity or the trophic complexity of any riverscape. Over and above the fragmentation of riverscapes by dams, canals and embankments, direct threats to vertebrate species (from hunting, poaching, targeted harvests in fisheries or fisheries by catch) can further obscure the understanding of the effects of climate change on river ecosystems. This is recapitulated in that direct killing has been one of the main contributors to the high extinction rates of freshwater biodiversity in the last century (see Antunes et al. (2016) for an example from Amazonia). Climate impacts can be coupled or uncoupled with ecosystem dynamics and the memory of historical perturbations, thus generating emergent and complex properties (Higgins et al. 2002; Woodward et al. 2010). To understand climate impacts, it is thus necessary to understand their interaction with non-climatic human-induced impacts on river biodiversity, whose magnitude and intensity can be significantly affected by global change (Palmer et al. 2008).

General Patterns

Impacts of climate change will be the strongest on ectothermic species such as fishes, amphibians, and reptiles, and will have important evolutionary implications (primarily extinction of specialized lineages). However, higher endothermic vertebrates, such as mammals and birds, would face a lower range of population- and community-level impacts. Ectotherms cannot regulate their body temperature according to the ambient environment, and hence they will be more sensitive to increased air or water temperature. The Bergmann's rule predicts that across latitudes (or altitudes), species' body sizes are greater in colder climates than warmer tropical climates. The fit of observed data on mammals and birds to this prediction has been tested by Teplitsky and Millien (2014), but they did not find compelling evidence at short time-scales for climate warming. However, reductions in body size have been noted either in relation to evolutionary scales of climate warming (over millions of years), or in relation to non-adaptive plasticity to abrupt environmental switches (e.g. temperature anomalies). Smaller ectothermic freshwater species are predicted to benefit from global warming, as they naturally occur in greater diversity in warmer tropical climates. Thus, warming could drive selection pressure on traits that allow for rapid turnover and low investment, and this could lead to size reductions of organisms, and affect individual fitness as well as community dynamics (Daufresne et al. 2009).

Climatic impacts on flow regimes of 'flood-pulsed' riverine ecosystems (Junk et al. 1989) can, however, strongly affect riverine species. In regulated rivers, differences between flood peaks and dry-season flows have either been inflated by water diversions or storage (in the case of irrigation dams), or flood peaks have been flattened (due to flood-control by barrages) (Dudgeon et al. 2006; Arheimer et al. 2017). Imbalances between surface water evaporation from warming, and higher melt-water or groundwater inflows into regulated rivers can significantly modify flooding patterns. The timing (of rise and recession), wavelength, amplitude, and duration of the flood pulse are critical cues for fish species to spawn or migrate, as well as for higher vertebrates to reproduce (Junk et al. 1989; Robertson et al. 2001; Dudgeon et al. 2006; Arthington et al. 2010). Annual and seasonal flood pulses 'subsidise' and enrich biological productivity, by facilitating nutrient and sediment fluxes into river channels through floodplain inundation. Flood stage (water levels) and river temperature are usually coupled (correlated) in rivers with dominant monsoonal precipitation, but can be decoupled (not correlated) in rivers where the relative contribution of dry-season snowmelt is high (Arthington et al. 2010). As water temperature is a stimulus for spawning and breeding, climate-driven and non-climate-driven impacts on flood-temperature coupling can substantially alter the reproductive success and fecundity of most vertebrate species.

In the following sections, we will examine the independent and synergistic effects of climate change driven and non-climatic factors on specific freshwater vertebrate taxa. The interactions between climate change impacts and impacts of direct or indirect (non-climatic) anthropogenic threats are summarised in a conceptual framework presented in Figure 7. The conceptual framework tries to identify how climatic and non-climatic drivers might affect specific life history stages or species sizes in particular contexts. It can be used to construct testable hypotheses about the impacts of climate change on freshwater biodiversity in human-dominated riverscapes.

Fish and Fisheries

Literature on climate change impacts on freshwater fishes is dominated by studies from temperate regions, because of available knowledge baselines and because stronger impacts of climate change are seen from colder regions. A study from the Rocky Mountains of USA estimated a range reduction of 10% to 75% from the present ranges of cold-water fish species in temperature increases of 1-5°C (Rahel et al. 1996). In southwestern Australia, endemic fishes of Gondwanan evolutionary origin evolved in cold climates, and thus may be prone to rapid extinction from increases in the mean and range of temperatures (Davies 2010).

Of course, the impacts that global freshwater fisheries have suffered from river flow regulation and fragmentation remain far more serious than future warming effects (Liermann et al. 2012). Water withdrawals have already been so severe that, as Xenopoulos et al. (2005) showed, unless water consumption is reduced at the global scale, it would be impossible to prevent large-scale extinctions of freshwater fishes (which are already the most threatened group of

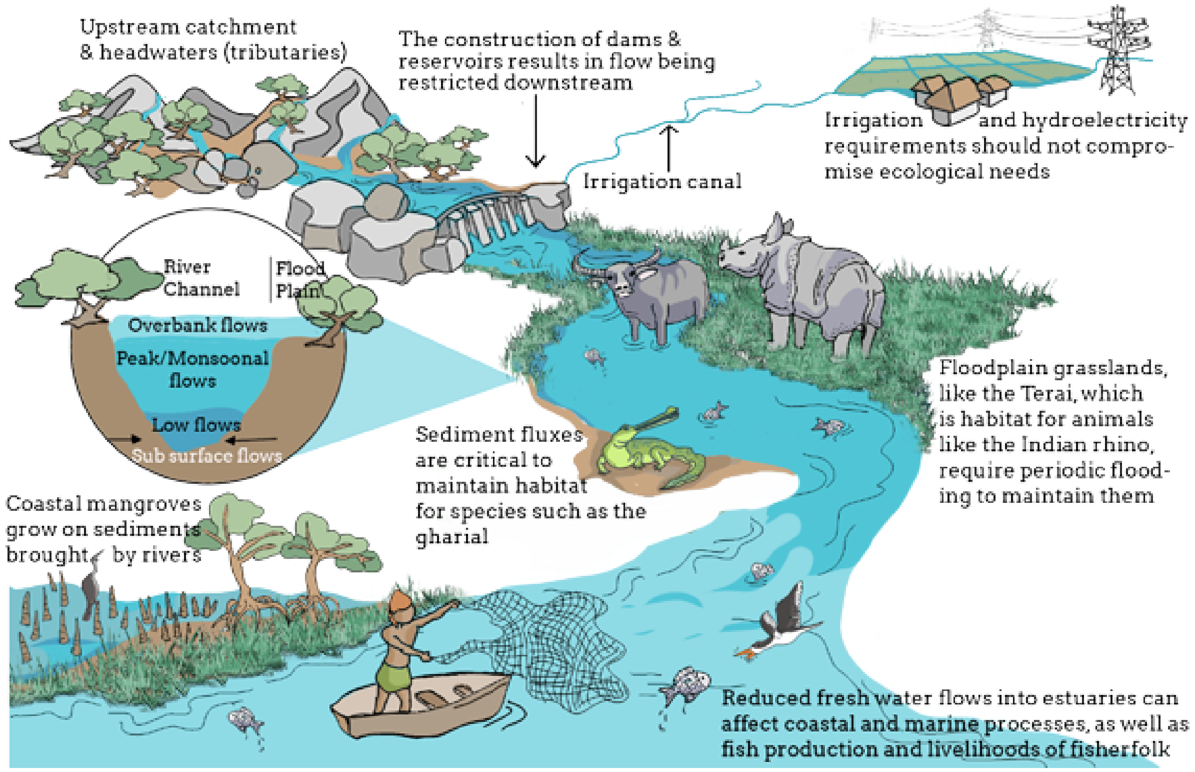


Diagram 1. Competing demands on river water resources in India. This schematic depicts a river's course from its headwaters to the ocean, and illustrates that ecological flow regimes are important to maintain habitats and biodiversity.' Credits: Megha Vishwanath, under a Creative Commons license

freshwater animals worldwide; Arthington et al. (2010); Liermann et al. (2012)). In rivers of peninsular India, where rates of water abstraction are extremely high compared to surface flows, major declines in fish species richness were predicted by 2070 (Xenopoulos et al. 2005). Scenarios of future warming and dam-building in the Indo-Burma fish hotspot (including the Mekong River) also indicated variable, but largely negative impacts on richness, community composition, and range extents of fish species (Kano et al. 2016). In India's Western Ghats – a high endemism and species-rich ecoregion for freshwater fish – rapid urbanisation and consequent stress on freshwater availability for urban uses are predicted to cause serious declines in fish diversity (McDonald et al. 2011). Overall, Indian riverine species appear to be the most vulnerable to the impacts of increased freshwater withdrawals, barring urban regions of eastern China, and naturally water-stressed regions such as Arabia.

Ficke et al. (2007) anticipate novel selective pressures acting on both the physiology and genetics of different fish species under climate change and warming scenarios. They propose that species along east-west flowing rivers will be exposed to similar risks along the same thermal isolines. Though simplistic, this prediction could be tested by including variables such as river catchment size, length, and anthropogenic impacts. The bottom line remains that climate change effects are expected to be severe, and aggravated by climatic extremes, for fishes already living in fragmented river systems.

Apart from the loss of native fish species diversity, climate impacts acting together with manmade impoundments and water withdrawals can encourage fish invasions into river systems. Invasion success has been high in rivers with severe flow regulation and more impoundment, perhaps due to stable seasonal temperatures (Havel et al. 2005), such as in the Upper Gangetic basin. In the middle and lower basin, where river flows suffer from less regulation, the same species that are now naturalized in the upper basin have not been able to establish. Fish invasions are well-known to be important threats not only to native fish diversity, but also to trophic interactions and river ecosystem processes.

The impacts of climate change on fish biology cannot be seen isolated from both the impact of commercial and artisanal fisheries on them, and the ecosystem services that riverine and wetland fisheries derive from them. Fished populations are known to closely track climatic fluctuations, because mature mega-spawning adults that can overcome proximate climate stressors have been fished out in all commercial as well as most artisanal fisheries. Trophic downgrading and size reduction by high-selective fisheries can be confounded with effects on allometry and fish growth arising from climate change (Daufresne et al. 2009). Note here how impacts of climate change at global scales can mimic local impacts of prolonged targeted fishing on larger fish species and individuals. As commercial fisheries exert their own selective pressures at the population and community level, and given the 'shifting baselines' in river fisheries, climate impacts on depleted stocks may be hard to detect.

In the Gangetic plains of India, recent increases in river water temperature are thought to explain altered spawn production of commercial fish species such as the Indian Major Carps (IMC) in the Gangetic basin (Vass et al. 2009). However, spawn declines have already been noted for IMCs due to overexploitation since the 1970s (Jhingran and Ghosh 1978). Field observations indicate that some small barb and catfish species, which are now the mainstay of artisanal fisheries in the Ganga River, might be breeding throughout the year, probably to compensate for altered cues for seasonal spawning (Kelkar, N. personal observation). The understanding of how El Niño Southern Oscillation (ENSO) and La Nina events might affect fish production in large rivers also remains poor, and offers an interesting area for scientific research.

From what is known, declining fisheries that are being hammered by elevated and extreme hydro-climatic regimes have raised concerns for sustainable fishery livelihoods. Badjeck et al. (2010) argue that the natural character of river fishing has always been in its inherent tracking of climate and weather uncertainties. Hence, mobile and flexible fisheries livelihoods, so far as enabling social policies and institutions to protect them, can provide vital insights and knowledge about climate adaptation and resilience. However, the commercial drive towards inland aquaculture fisheries in Asia, although generating more cash flows and livelihoods, could compromise the capabilities of 'settled' fishing communities to adapt to extreme climate variability.

Reptiles

Bickford et al. (2010) predict "severe and irreversible impacts" on herpetofauna under climate-driven temperature shifts and reduced freshwater availability. As amphibians are sensitive to desiccation, predictions of "warmer and drier" tropical climates indicate their high susceptibility. Multiple developmental stages of amphibians are linked to temperature and precipitation cues, which in turn determine biochemical stimuli. With increased drought-lengths and rainfall extremes, a range of vital traits and behaviours can get affected. Increased fungal disease risk to amphibians has now become a pan-tropical problem, and climate change has had a role to play in its transmission and prevalence in several amphibian populations. Ectothermy enforces additional constraints on metabolism: while amphibians depend on moisture and must avoid skin desiccation, crocodile and turtle thermoregulation depends on basking duration. Predicted changes in ambient weather (e.g. higher fog persistence, wetness, etc.) could reduce thermoregulation opportunities, especially in harsh winters.

Ihlow et al. (2012) predicted large-scale niche shifts, range contractions, and reduction in local species richness of freshwater turtles, driven by altered temperature regimes interacting with habitat loss and causing reproductive failures. Increasing incident solar radiation and hotter sand temperatures can affect egg development and sex determination (TSD: temperature sex determination) in turtles and crocodiles. In these reptiles, the nest temperature determines the sex ratio of the hatched brood. In crocodiles, lower temperatures typically lead to females and higher, stable temperatures lead to males, but inter-species variations exist. In turtles, three types of TSD exist (female-warm, male-female, female-extremes-males-means; Parrott and David Logan (2010) and the adaptive capacity of each type to resist dramatic changes in sex ratios and population recruitment can be quite different.

In both TSD and non-TSD reptiles, increased temperatures due to air warming, soil drying, and shorter and fluctuating hydro-periods have affected sex ratios, which is a grave concern (Bickford et al. 2010). Nesting failures in riverine crocodile species are known to be associated with fluctuations in ENSO-driven flood events and unstable temperatures (Herrera et al. 2015). The gharial crocodile of the Indian subcontinent has been critically endangered by historic hunting and fishing impacts, habitat loss and altered river flows, with only a few hundred breeding adults left in the wild at best (Choudhury et al. 2007). The gharial nests in sand banks, and warming nest temperatures might be a serious issue for remnant populations, and research is needed on the role of climate change impacts in altering sex ratios of gharial hatchlings.

Other impacts of modified flood pulses are likely to be seen in specialist breeders such as the crowned river turtle *Hardella thurjii*, thought to lay eggs in the water. This turtle times its clutches so that receding post-flood water levels expose the eggs to the exact hatching temperature. Whereas severe hunting has decimated populations of soft-shelled turtles and some hard-shelled turtles in the Gangetic plains, *Hardella* is perhaps an exceptional case, which local fishers attribute to alterations in the flood recession phase of the river. The species, however, is doing well in floodplain wetlands and ponds, where recession periods may be stable, in the Upper Ganga basin.

Birds

Changes in migration timings and extent of seasonal movements along major flyways, widespread habitat loss, and impacts on breeding success have been noted for waders and waterfowl, in response to rising temperatures (Maclean et al. 2007). Warming in the Northern Hemisphere, thawing ice in tundra lakes, and changing precipitation at higher latitudes might also threaten breeding grounds of waterfowl. A study from the Odra estuary on the Baltic Sea coastline showed that increasing snowmelt particularly affected piscivorous duck species (Marchowski et al. 2017). Moderate to high vulnerability to climate change was predicted for almost one-third of the wetland bird species in the USA (Reese and Skagen 2017). Bird species dependent on river flows for nesting, such as sandhill cranes, show high susceptibility to increasing drought frequencies and earlier spring flows due to changes in snowmelt rates.

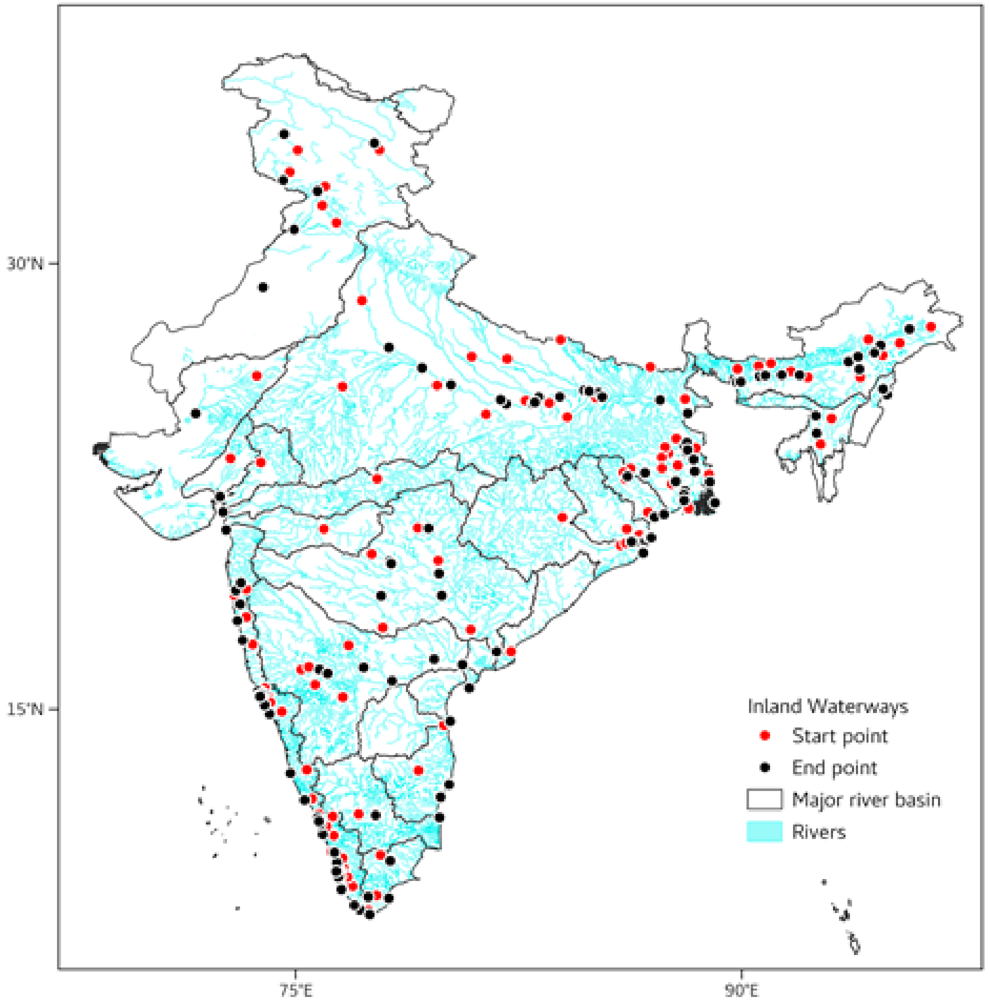


Figure 6. Emerging threat, National Waterways. The red points show the approximate end-points of the 111 waterways proposed in the National Waterways Act, 2016. This map is only for indicative purposes. Due to large-scale modification of rivers, almost 90% of the endangered Ganges river dolphin's habitat is in danger. Of the rivers that are home to the last four wild breeding populations of critically endangered gharials in the world, two are planned for full conversion to waterways. Birds like the Indian skimmer that depend on undisturbed river stretches will be further threatened. There is already very little water in most of the peninsular rivers for waterways development to be possible. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

In India, it has been shown that altered monsoonal patterns might also affect availability of food resources for group-nesting wetland birds (Urfi 2011). Birds that use river island habitats for breeding to protect eggs and chicks from terrestrial predators (e.g. dogs, jackals, etc.) also need specific thresholds of river flow during the breeding season. In cases where flows increase, nests can get inundated, and when flows reduce drastically (as in prolonged droughts), easier predator access can lead to successive breeding failures. This is likely to be the case for vulnerable bird species such as the Indian skimmer. Birds dependent on coastal wetlands are also predicted to suffer from sea level rises, and the same is probable for seabirds nesting in colonies on remote sea sand-spits or around tropical oceanic islands (Maclean et al. 2007).

Mammals

Obligate freshwater mammals include only the true river dolphins: the Amazon, Bolivian, and Araguaian river dolphins of South America (until recently considered the same species), the now extinct Chinese river dolphin or baiji, and the Indus and Ganges river dolphins found in South Asia (India, Pakistan, Bangladesh, Nepal). All other 'freshwater mammals' are either largely – but not completely – dependent on rivers, wetlands, and estuaries (e.g. otters, with 12 species worldwide, excluding the sea otter; the Baikal seal, hippopotamus, and three species of manatees that occur along the Atlantic coasts of Africa and the Americas), or are facultative users only (e.g. semi-aquatic rodents, water shrews, fishing cat, small carnivores that re-adapted to fishing, etc.). Highly specialized and range-restricted mammals such as the Baikal seal are obviously threatened by thawing ice and increased precipitation in Siberia. Otters or hippos, on the other hand, despite their major dependence on rivers, might not be affected much by regular climate change impacts. Otters show high behavioural plasticity and can adapt to a range of habitats, including marshy or swampy lands, agricultural fields, and even semi-urban water bodies. As a result, no impacts specific to climate change on these and other facultative freshwater mammals may be anticipated.

This leaves only river dolphins as the prime examples of mammals whose habitats might witness serious climatic stressors. In particular, the Indus and Ganges river dolphins in South Asia are expected to show further range declines in response to weakening monsoons and decreasing river discharge across their ranges (Learmonth et al. 2006). Among these two (sub-) species, Indus dolphin populations in Pakistan might be under severe stress. The annual discharge of the Indus comprises of about 50% glacial melt waters, which is higher than for any large river originating from the Himalaya or Tibetan Plateau (Zhang et al. 2013). To top that, the Indus has been shackled by six major barrages along its length, which has reduced the range of the Indus dolphin by 80% of the original distribution (Braulik et al. 2014). Under scenarios of climate-induced drought in the semi-arid Indus basin, it is evident that this species is going to face extreme stress in the near future. The Ganges river dolphin also suffers from similar impacts in the Ganga-Brahmaputra basins of the other range countries, but its larger distribution range and the lower density of barrages provide it with better chances.

Ganges river dolphin (Platanista gangetica) *(Photo: Zahangir Alom/Marine Mammal Commission/Oceanic and Atmospheric Administration; Wikimedia Commons)*

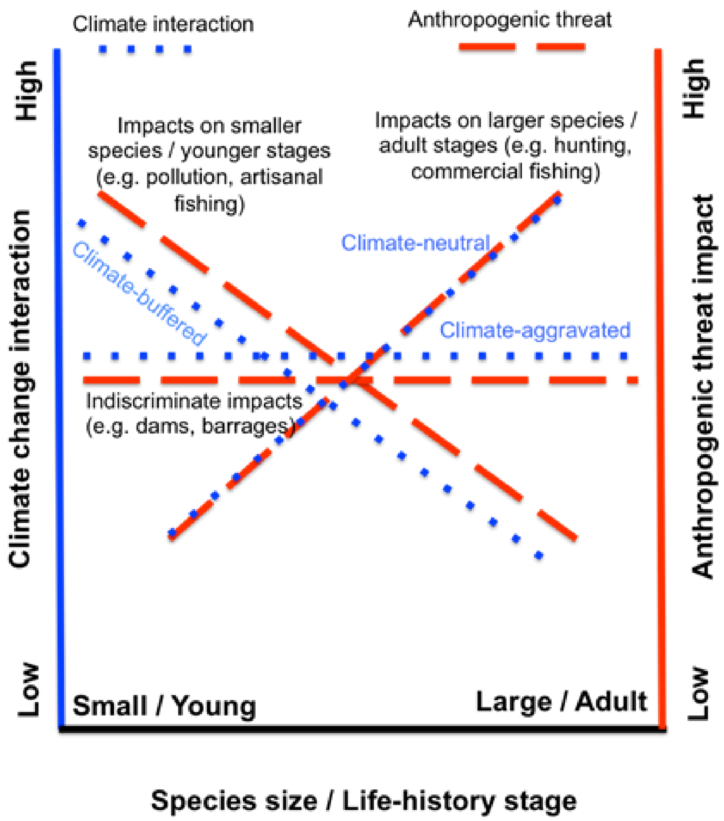


Figure 7. A conceptual framework showing impacts of direct anthropogenic threats in relation to species size or life history stage (i.e. small species/young animals or large species/adult animals), and their interactions with climate change (shown as lines with positive, negative, and zero (neutral) slopes). Red dashed lines indicate examples of specific anthropogenic threats. Blue dotted lines indicate examples of how climate change effects might alter threat impacts on species: (1) climate-aggravated; where indiscriminate impacts such as those of river flow regulation could be worsened by climate change, (2) climate-buffered; where younger stages might become less vulnerable to pollution levels due to dilution by enhanced flows (e.g. rapid snowmelt increases), and (3) climate-neutral; where direct, targeted threats such as hunting of large species or adult animals may have little or no interaction with climate change impacts

Apart from dams, river dolphins in South Asia are under significant threat from fishing bycatch mortality, river pollution, and emerging stressors such as industrial river waterways (in India and Bangladesh), which are gradually increasing levels of anthropogenic noise in their habitat (Kelkar 2017). Almost 90% of river dolphin habitat overlaps directly with the proposed extent of waterways development (Figure 6), and will be affected by dredging and associated impacts. Climatic stressors could aggravate the impacts of such threats.

For the South American river dolphins, population declines have been primarily from targeted hunting and killing, rather than habitat loss or climate change. In fact, for all river dolphins, which are among the world's most endangered cetaceans, the ultimate alarm comes from the recent human-caused extinction of the Chinese river dolphin or baiji (*Lipotes vexillifer*). The primary reasons for this extinction were mortality due to the use of destructive electric rolling fish hooks, targeted and accidental killing, and the development of the Yangtze River as an industrial waterway since the 1950s (Turvey 2008). The Three Gorges Dam on the Yangtze contributed to the extinction, but only in a minor way.

But the dam had a larger impact on the functional extinction of large river fishes like the Chinese sturgeon, while hunting and fishing impacts have now claimed almost all wild populations of the Chinese alligator and Yangtze soft-shell turtle (Turvey 2008). The dam also drastically reduced the freshwater availability in Poyang lake (China's largest; Mei et al. 2016), which now threatens Siberian cranes that overwinter there. Tragic extinctions of the Yangtze River's biodiversity should remind us why climate change is not such a serious issue for the conservation of species which are endangered by non-climatic factors. In fact, the issue of climate change might distract conservation policies from tackling more serious current threats to endangered species.

Are 'Direct Threats' Completely Climate-Neutral?

As we have seen, direct threats from targeted hunting, or accidental bycatch have had large impacts on riverine reptiles and mammals, probably independent of climate change. But today, even threats need not be entirely delinked from climate impacts. For instance, during droughts and reduced river flows, accessibility of hunters and poachers to river floodplains might increase. Drought-induced famines could also significantly aggravate local human dependence on river animals. A study on Ganges river dolphins from Nepal (Khanal et al. 2016) suggested that the risk of accidental entanglement and mortality in fishing nets increased in sudden low-flow situations. Prolonged drought could aggravate mortality by forcing species towards greater overlap with fisheries activity – and leading them into 'ecological traps'.

In many areas, populations have probably already gone beyond the threshold for natural recovery, such as in the case of the gharial crocodile. Assisted recovery by captive-bred animals has been attempted, but has largely been a failure due to poor monitoring, in the face of the pernicious extent of habitat loss, hunting, and fishing (Choudhury et al. 2007). Considering that monitoring and law enforcement have been unable to control direct threats, their capacity for arresting indirect threats from climate change appears further more insignificant.

IMPACTS OF CLIMATE CHANGE ON AMPHIBIANS AND FRESHWATER MOLLUSCS

The increasing temperature and changes in precipitation patterns due to climate change will have a severe impact on freshwater ecosystems. The degree to which an ecosystem responds to climate change will depend on the ecoregion (e.g., cold, temperate or warm), type of ecosystem (e.g., lakes, rivers or wetlands), and on individual species' adaptation to the environment. Freshwater biodiversity is highly vulnerable to climate change (Woodward et al. 2010; Poff et al. 2012). Key reasons include climate dependence of thermal and hydrological regimes, limited dispersal ability of many freshwater organisms, and additional stressors such as habitat loss, pollution, harvesting, river regulation, over-abstraction of water, introduction of alien invasive species (Woodward et al. 2010), and emerging infectious diseases in aquatic organisms such as chytrid infections in amphibians. There is good recent evidence of ecological consequences of climate change on various taxa - including shifts in the distribution, range contraction, population decline and local extinction (Stuart et al. 2004; Comte et al. 2013; Domisch et al. 2015). In this section, we synthesize the impact of climate change on amphibians and freshwater molluscs at the national and international level.

Amphibians

Species belonging to order Amphibia (which includes frogs, toads, caecilians and salamanders) are sensitive to changes in the environment due to their highly permeable skin and unique biphasic life cycles (Stuart et al. 2004; Ochoa-Ochoa et al. 2012). Amphibians are highly sensitive to climatic changes because of their ecological, behavioural, and physiological attributes (Blaustein et al. 1994; Stebbins and Cohen 1995; Stuart et al. 2004; Hof et al. 2011; Ficetola et al. 2015). Temperature and rainfall are two climatic factors critical to amphibian physiology and behaviour, because of their role in gametogenesis and reproductive migrations (Noble 1931; Beebee 1995; Todd and Winne 2006). It is well known that (1) climate change predictions vary considerably with geographic locations, (2) there is a high degree of uncertainty with all climate change models, and (3) being a diverse taxon, there is no single or simple answer to how amphibians are likely to respond to climate change (Olson and Saenz 2013). Studies have shown that climate, coupled with land-cover change will alter future thermal landscapes of amphibians, reducing suitable areas as species increasingly encounter temperatures that exceed their thermal tolerances (Nowakowski et al. 2017).

Amphibians are the most threatened groups of animals on earth with almost 25% (2000 species) of some 7,932 currently known amphibian species (Frost 2018) threatened with extinction (Stuart et al. 2004; Hof et al. 2011). It has been estimated that 3.1% of amphibian species have already gone extinct since 1700 AD (Alroy 2015). The study also suggested that extinction rates are now four times higher than the background rate, and at least another 6.9% of all frog species may be lost within the next century (Alroy 2015). Climate and land-cover change are reshaping the distributions of species and the structure of native communities (Colwell et al. 2008; Sheldon et al. 2011; Newbold et al. 2015). Climate change has been hypothesised to have severe synergistic effects on amphibian decline, considering that it may exacerbate the negative effects of anthropogenic habitat loss, fragmentation and land-use change (that may increase amphibian extinction risk).

Climate change can alter the distribution of species by causing shifts in the area, latitude, longitude and/or altitude, and thus impact their geographic ranges (Pearson and Dawson 2003; Raxworthy et al. 2008). The range changes can impact ecosystem functions and biodiversity (Raxworthy et al. 2008). The behaviour, reproduction, and physiology of amphibians are highly temperature-dependent (Wells 2007). Thus, thermal gradients affect their habitat selection (Freidenburg and Skelly 2004) and movement (Nowakowski et al. 2015), thereby shaping amphibian distributions (Frishkoff et al. 2015). Locations and regions with many endemic or endangered species such as India are more sensitive to climate change (Malcolm et al. 2006). The amphibian chytrid fungus is also recognised as a major threat to frog populations worldwide (Skerratt et al. 2007), but the role of climate change in current chytrid fungus-related extinctions is not clear yet (Pounds et al. 2006; Rohr et al. 2008). Given that the growth and impact of chytrid infections are strongly temperature-related (Berger et al. 2004), it is highly likely that climate change will increase the future spread of disease in some areas, whilst reducing them elsewhere.

Scutiger sikkimensis *from Sikkim (Photo: Subba, B., Ravikanth, G., and Aravind, N. A.; Wikimedia Commons)*

Much of our understanding of climate change impact on amphibians comes from the US, Europe or other temperate regions such as China, with only a very few studies from tropical regions such as South America, India or South East Asia. Amphibians in China (on an average) would lose 20% of their native ranges. However, the distribution outside current ranges would increase by 15%. The study also predicts two different general responses to climate change: some species contract their ranges while moving westwards, southwards and to higher altitudes (niche shift and contraction), while others expand their ranges (expansion). Most of these shifting range species are distributed in forests, farmlands and wetlands (Duan et al. 2016).

Habitat suitability within species ranges was predicted to decrease in the future for amphibians of California, USA. The study from Europe using species distribution modelling methods forecasted a general reduction in species' ranges, leading to a decrease in the number of sites with high species richness. Most species studied had a significant range contraction (up to 85%) and 12% of species were expected to be regionally extinct (Loyola et al. 2014). In Costa Rica, 16-30% loss of suitable habitats under climate and land-use change scenarios was predicted (Nowakowski et al. 2017).

A recent study from the Western Ghats of the endemic species *Nasikabatrachus syhadrensis* (Nasikabatrachidae) shows that there will be a shift in its distribution under the Representative Concentration Pathway (RCP) 8.5 scenario (Charles et al., manuscript Under Review). A similar result has been shown for the Himalayan frog genus *Scutiger* spp. (Barkha 2018). Invasive frogs have been shown to shift their ranges in response to climate change, as shown for the species *Lithobates catesbeianus* (López et al. 2017). Some modelling studies also showed that several amphibian species will expand their ranges in response to climatic warming in Europe. However, the ability of amphibian species to cope with climate change is dependent on the availability of water, and the species' ability to disperse (Araújo et al. 2006).

Apart from range shift and contraction, reproductive phenology also seems to be affected by climate change. Previous work has shown earlier breeding in several amphibian species in response to recent climate warming (Beebee 1995, 2002; Gibbs and Breisch 2001). A recent study by Todd et al. (2011) has shown that there is early and delayed reproduction in 10 species of amphibians, in relation to climatic warming over the last three decades in Europe. However, no consistent pattern has been observed in North American amphibians (Blaustein et al. 2001). For Indian amphibians, no such long-term data is available.

Availability of water in amphibian breeding habitats such as temporary, ephemeral, or vernal ponds and intermittent or discontinuously flowing streams is particularly important for breeding and survival (Olson and Saenz 2013). Earlier studies have shown that many amphibian species are already experiencing mass mortality of eggs, tadpoles, and metamorphosing individuals due to desiccation (Blaustein 1991). Extreme rainfall will only worsen the situation. Extreme rainfall events which are happening in many parts of India will have a negative impact on the breeding phenology of aquatic breeding frogs of the Western Ghats and Himalaya (Figure 3). Climate change may result in shifts in reproductive behaviour, especially for species that breed early during the monsoon season (e.g. *Nasikabatrachus* spp.) or late (e.g. *Micrixalus* spp.). A shift to earlier breeding may leave amphibians exposed to fluctuating weather conditions (extreme temperature or precipitation). Some aquatic habitats can act as 'stepping stones' for dispersal between sites after breeding. So, altered hydroperiods can have negative effects outside of reproductive losses (Olson and Saenz 2013), thus impacting local population size. Another side effect of changed hydroperiod could be increased vulnerability to predators.

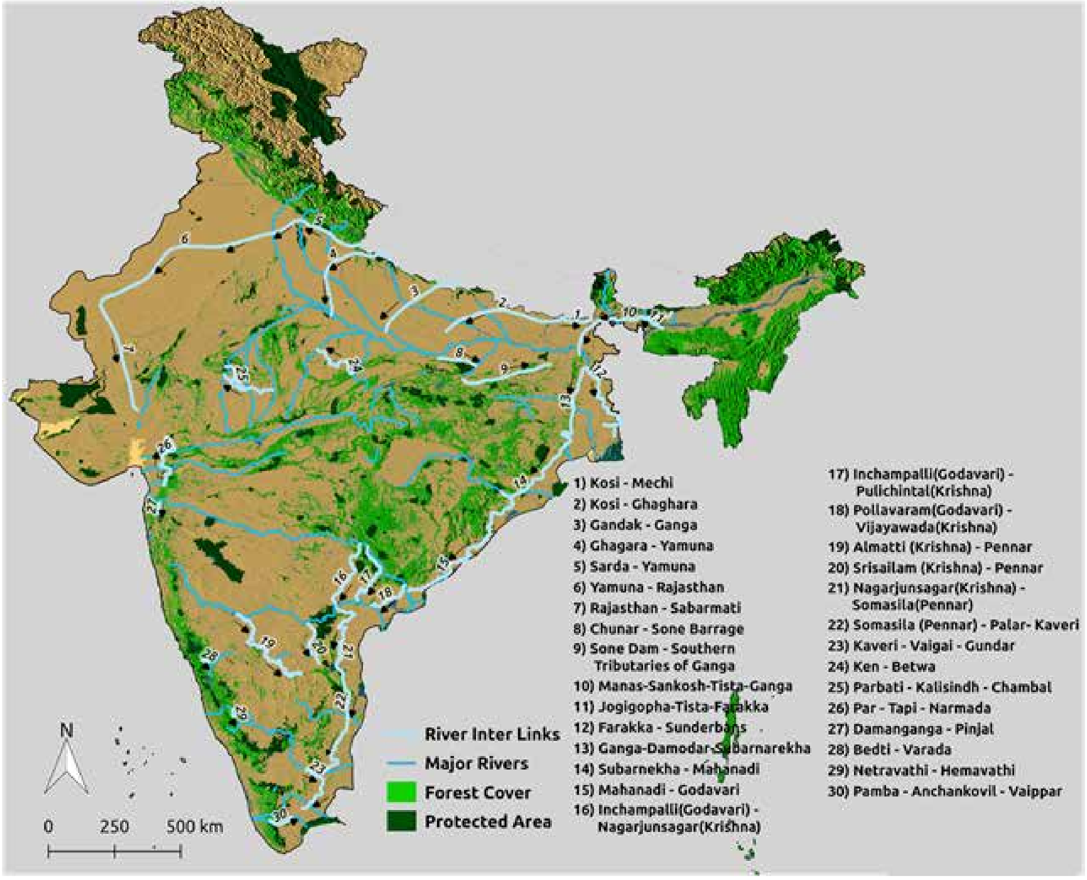


Figure 8. River interlinking projects will rip through 180 km of Protected Areas and 1100 km of forests. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

Freshwater Molluscs

Freshwater molluscs belong to two phylogenetically distinct lineages, i.e., Gastropoda (snails) and Bivalvia (clams). They are one of the most important components of macroinvertebrate assemblage in freshwater ecosystems. Molluscs, which form an important link in aquatic food webs and help to recycle nutrients, are considered ecosystem engineers. Given the limited dispersal ability of freshwater molluscs, those which are restricted to lotic habitats are much more vulnerable than those in lentic habitats. The situation is even more critical for bivalves as their reproduction is dependent on host fish species – as they require larvae to parasitize on the gills of fish for the development of young ones. Global studies on the impact of climate change on freshwater molluscs (both bivalves and gastropods) are meagre. Much of our understanding (again, like in the case of amphibians) comes from the temperate regions (such as Europe and North America). Studies from tropical regions are either rare or almost absent.

A study from pan-Europe on freshwater molluscs have predicted that this group is the most heavily impacted by climate change among all freshwater groups assessed. This study showed that almost 60% of freshwater molluscs, most of which are rare, are classified as being under "imminent threat" from climate change (Markovic et al. 2014). Another study has shown that the range and abundance of freshwater pearl mussel (*Margaritifera margaritifera* (L., 1758)) has declined significantly in the last century across Europe (Bolotov et al. 2018) Increasing evaporation, lower oxygen concentration due to increased water temperature, and changes in precipitation pattern are likely to affect the survival of freshwater molluscs (both gastropods and bivalves).

Studies from North America show that young mussels have difficulty in surviving in higher water temperatures, and that this may happen more frequently in the future in North America's rivers and lakes, due to

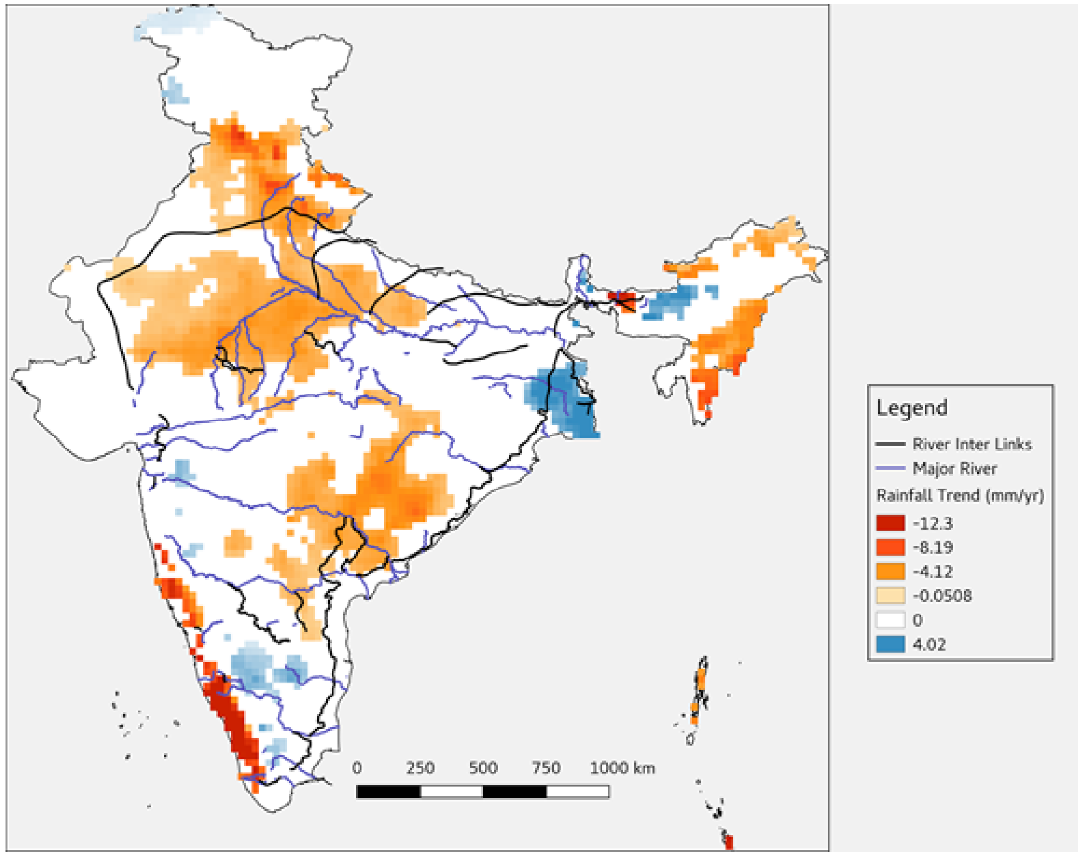


Figure 9. River interlinking projects are largely concentrated in basins that show historical declines in rainfall. Disclaimer: this map is for illustrative purposes only, and does not reflect actual international boundaries.

Box 1
Adapted from report called: Defining Ecological Flows for Karnataka

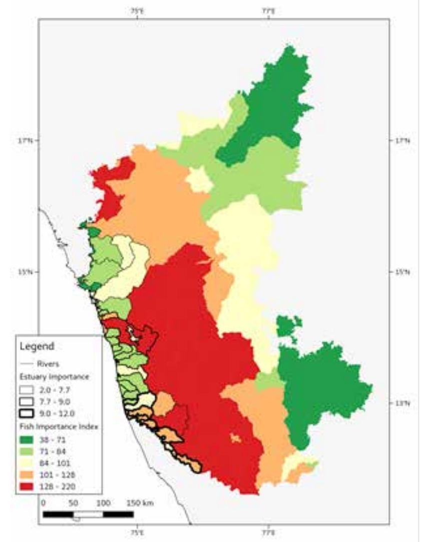
Ecological flows are required for the maintenance of natural river flow regimes, sustenance of aquatic biodiversity including animals and vegetation, groundwater recharge, prevention of salinity incursion (into agriculture and settlements) and maintenance of estuarine conditions, in addition to supporting water-based livelihoods, and the cultural and spiritual needs of people. It is well documented that flow alteration is associated with ecological change, and the risk of ecological degradation increases with increasing magnitude of flow alteration.

Using long-term flow data from Barbarossa et al. (2018), we defined and tested two indices. 'Lowflow' at any site in a regulated river stream was defined as the 50th percentile of the long-term modelled minimum annual flow time-series under unregulated conditions. We also defined the 90th percentile of mean annual flows as another index called 'Averageflow90'.

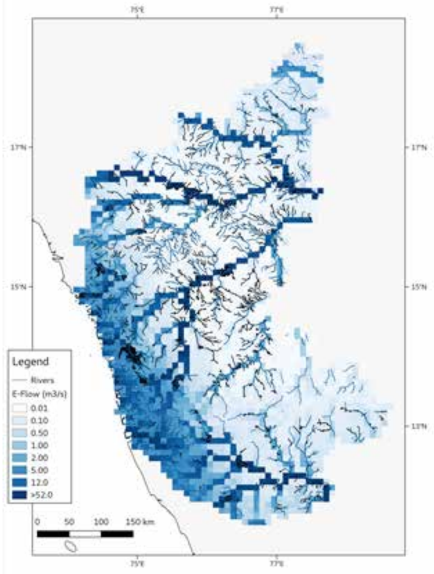
For each basin, the vulnerability of fish species to flow conditions was ranked based on the generally understood trend that bottom dwellers are least impacted (rank=1), followed by mid-column, (rank=2), and surface dwellers=3 (most susceptible), multiplied by IUCN threat category (Critically Endangered =5 to Least Concern =1) and summed up across the species known from each basin. We have called this the 'Fish Importance Index'.

We fit linear regression models with Fish Importance Index as the response variable, and with the following predictor variable combinations for comparison: Lowflow, latitude and elevation, and another with Averageflow90, latitude and elevation. The model results were significant in their effect on Fish Importance Index, but the model with Averageflow90 as a covariate was stronger than other models. Models with average flow did not show significant effects. Therefore, the ecological flows for Karnataka was estimated using the Averageflow90 index.

Under future climate change and scenarios of small dams and abstraction of river water, maintaining these ecological flow regimes will be necessary to conserve aquatic biodiversity, fisheries and ecosystem services of rivers and streams.



Prioritized catchments based on the Fish Importance Index and number of estuarine species found in the catchment; thickness of the line indicates the importance of the catchment for estuarine species.



Averageflow90, the 90th percentile of mean annual flows was adopted as the ecological flow (E-flow) based on ecological criteria increased global temperatures (Ganser et al. 2013). A study from Zimbabwe showed that climate change may result in reduced spatial distribution of suitable habitats for selected freshwater gastropods (Pedersen et al. 2014). Several studies also showed that many freshwater mussels are currently living near their upper thermal limits. The response of molluscs to increased water temperature would be either to bury deep inside the mud or go locally extinct (Ganser et al. 2013).

In India, there are no studies on the impact of climate change on freshwater molluscs (Aravind et al. 2011). A recent assessment by the IUCN has shown that only half a dozen species are threatened, and about 40% of a total of 210 freshwater molluscs in India have deficient data. Given high endemism (around 40%) in both the groups (Gastropoda and Bivalvia) and considering that many of them have very narrow distribution ranges in the Western Ghats and in the Himalaya, any change in the temperature or flow regime will have an impact on the local population, especially in endemic genera such as *Cremnoconchus* and *Pseudomulleria*. Since bivalve molluscs are highly sensitive to changes in water chemistry and flow regime, any changes in the flow will not only affect mussel populations, but also host fish species. The ambitious river-linking project (Figure 8 and 9) and damming will only increase existing threats to freshwater molluscs in India.

For many aquatic macro-invertebrates, we have insufficient information on species' ecology. This lack of knowledge has limited our understanding of organisms' responses to changing climate. Understanding species' upper thermal tolerance limit is urgently needed to assess the response of communities to global climate change. Altered flow regime, changes in the temperature of freshwater systems due to climate change, harvest and pollution, coupled with land-use changes and the introduction of invasive alien species will seriously affect narrow-range endemics, habitat specialists and high-altitude species in the Western Ghats and Himalayan biodiversity hotspots. Species distribution modelling (SDM or ecological niche modelling) along with field and lab-based studies and long-term monitoring will help us understand species' response to climate changes in these two highly vulnerable freshwater taxa. Quantifying the general trends of the climate change-driven shifts in species distribution and abundance is extremely important for adequate conservation action and policies. However, despite the high endemism and richness in the above two taxa, to our knowledge, there has been no attempt to study climate change-driven shifts in distribution and change in abundance. Hence, there is an urgent need to study the climate-driven impacts on freshwater invertebrate taxa.

SYNTHESIS AND FINAL CONCLUSIONS

The current threats to freshwater biodiversity from non-climatic stressors and drivers are so intense and large-scale that the climate change impacts are less visible. However, climate change may lead to further trade-off between aquatic biodiversity and other demands for water and transformation of riverine ecosystems. There is an urgent need to recognise the ecosystem services of aquatic ecosystems, and put in place policies for assessing the irreplaceable losses of biodiversity from large-scale transformation of India's last free-flowing rivers. Policies to maintain ecological flow regimes from headwaters to estuaries (Box 1), as well as reducing non-climatic stressors on vulnerable biodiversity and careful monitoring of adaptation and mitigation opportunities at all spatial scales is needed.

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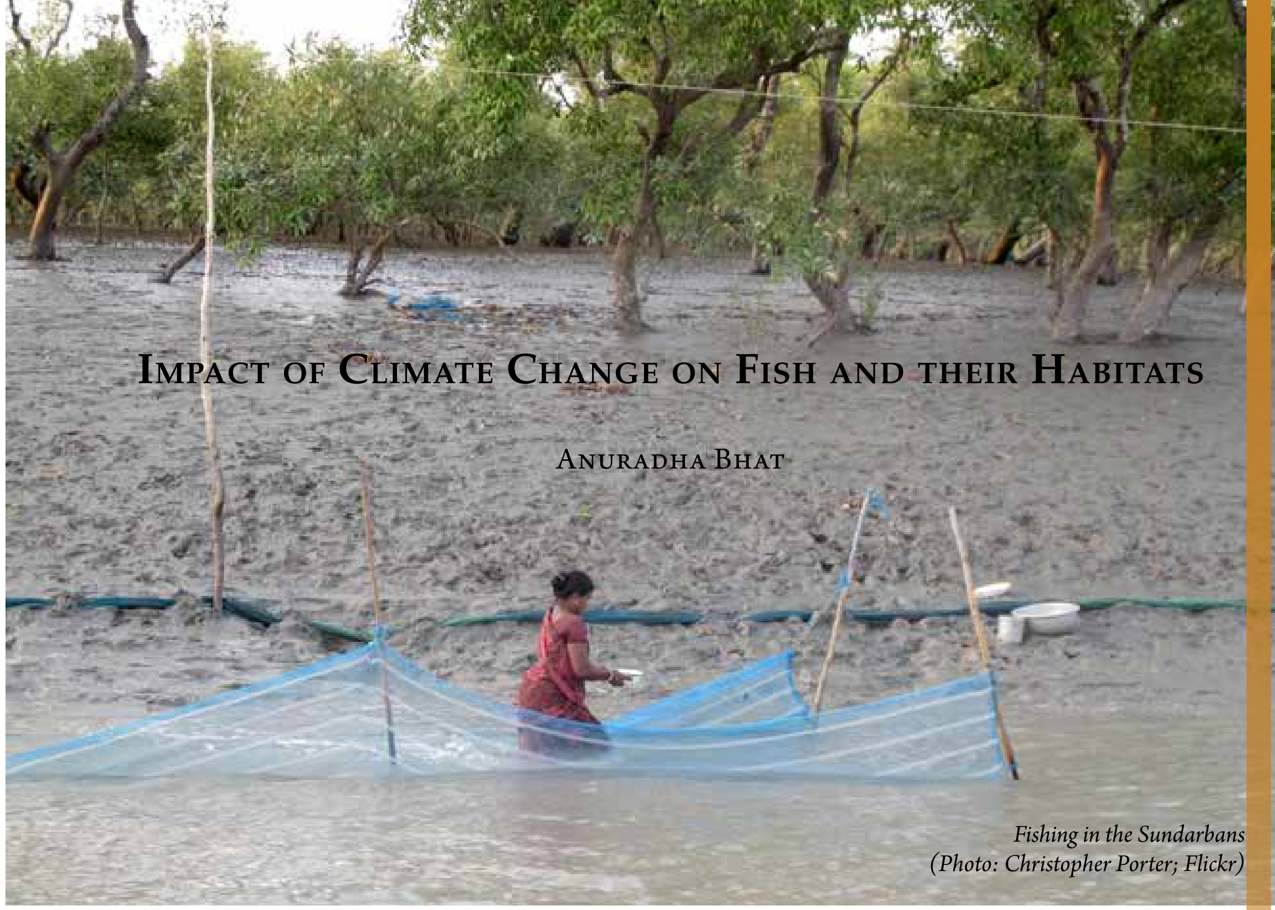
IMPACT OF CLIMATE CHANGE ON FISH AND THEIR HABITATS

ANURADHA BHAT



Fishing in the Sundarbans
(Photo: Christopher Porter; Flickr)

Habitat destruction, over-exploitation, invasive species and chains of extinction, famously referred to as the 'evil quartet' (Diamond 1984), are the major drivers of species extinctions in ecosystems across the globe. To this list of global threats to biodiversity, a relatively recent addition is climate change. The projected climate change scenario of a 2°C rise in temperature will impact aquatic fauna of both freshwater and marine ecosystems. Species living in freshwater ecosystems are particularly vulnerable as aquatic fauna typically have limited dispersal abilities. Besides, both water quantity and quality are climate-driven, and these systems are facing immense anthropogenic and environmental stresses (Woodward et al. 2010). While extended drought periods can impact mean water temperature and result in habitat fragmentation, extreme flood events can also alter the habitat connectivity and increase the water flow above threshold levels (Leigh et al. 2015). Studies over the last few decades have pointed to clear impacts of temperature rise on species distributions (Parmesan and Yohe 2003; Thomas et al. 2004). Ocean acidification and sea level rise are projected to impact as many as 1600 species of reef fishes. Even as marine biodiversity is affected, distributional shifts due to climatic changes can be expected to occur for several freshwater fish species in the coming years.

Fish habitats are characterised by several abiotic factors such as habitat structure, water flow and temperature, and biotic factors such as trophic relationships. As thermal regimes within aquatic habitats change, increase in water temperature can have major impacts on fish metabolism and activity. Temperature rises above tolerance limits of fish species can potentially result in rapid declines or even disappearance of sensitive species from these habitats. Studies conducted on fish species native to North American streams show a greater impact of these temperature rises on cold water fishes compared to warm water ones, as cold water streams are expected be warmed more than warm water streams if the climate becomes warmer (Eaton and Scheller 1996; Mohseni et al. 2003). As habitats for cold water species shrink, distribution patterns of species are likely to shift in the coming decades. Even as fish habitats affect these species, climate change will impact tropical freshwater species, especially riverine ones, in terms of changes in water quantity, due to increased seasonal fluctuations in river discharge. Frequent fluctuations would change habitat availability as well as oxygen levels, and this can affect sensitive species in these ecosystems.

Research on the impacts of climate change on freshwater systems within India is limited. However, the few studies so far conducted on species relevant to fisheries and aquaculture are already showing signs in terms of declines in fish stocks and shifts in distributions. Impacts of climate change in the Indian subcontinent can already be discerned through recent examples of increased air temperatures, regional variation in the monsoon, frequent occurrence of droughts, and a regional increase in severe storm incidence in coastal states. A 32-year time series data analysis showed a 0.99°C increase in the minimum water temperature in the upper stretch of River Ganga and a 0.5 -1.4°C increase in aquaculture water on the Gangetic Plains of West Bengal (Das et al. 2013). These changes have been reported to have shifted the distributions of warm water fish species such as *Glossogobius giuris*, *Xenentodon cancila* into the upper, colder stretch of the river. In the Himalayan river systems, changes in atmospheric temperature – and subsequently aquatic temperature – can already be seen with the rapid retreat of Himalayan glaciers, increased variability in precipitation as well as frequency of extreme events (Gopal 2013).

It is not just freshwater systems that are likely to face threats of changing temperature – ecologically sensitive coastal ecosystems such the mangroves along the Indian subcontinent are also likely to feel the 'heat' in the coming years. While some species are likely to be more tolerant of changes in water temperature and salinity, more sensitive species are likely to decline in numbers. For example, increasing salinity and temperature in mangrove habitats such as the Sundarbans are altering fish reproductive behaviour, and can result in rapid declines in the abundance and even extinction of local fish species (Pabda *(Ompok pabda*), Tangra (*Mystus gulio*), *Notopterus* spp.), many of which are of high commercial value (Chand et al. 2012).

Current climate change scenarios from general circulation models (GCM) indicate that the projected change in precipitation is the greatest for the tropics, while the projected air temperature change is the smallest. While most climate change scenarios indicate that regional precipitation will change in the tropics as the global temperature rises, the direction of projected change in regional precipitation varies among the GCMs. We can expect a wide variation in the range of impacts to riverine habitats, as rainy and dry seasons across different tropical regions could either become more severe or more moderate in the coming years. This can have important global implications for highly valued riverine fisheries, as well as several native and sensitive species. This is a critical time for us to develop accurate assessments of these impacts to our fish fauna and obtain analytical predictors of species and population distributions. Specific conservation programs can then focus on those species that are likely to be most vulnerable.

Bronze featherback (Notopterus notopterus) *(Photo: Ajiman; Wikimedia Commons)*

Tank gobi (Glossogobius giuris) *(Photo: Wibowo Djatmiko; Wikimedia Commons)*

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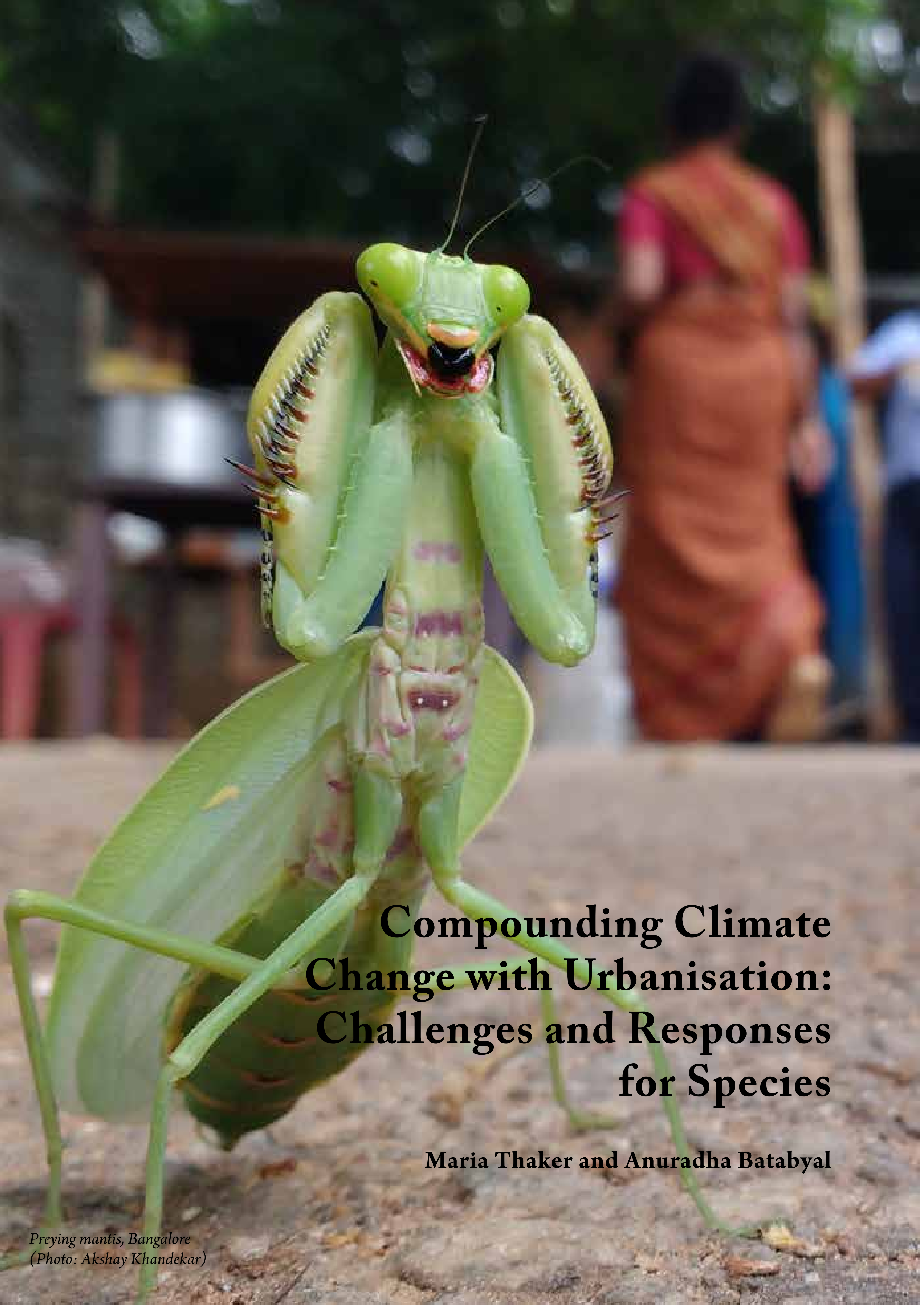

Compounding Climate Change with Urbanisation: Challenges and Responses for Species

Maria Thaker and Anuradha Batabyal

Preying mantis, Bangalore
(Photo: Akshay Khandekar)

INTRODUCTION

Since the evolution of eukaryotes, changes to climate and natural habitats have occurred at a pace that has allowed the evolution of coping mechanisms. The era of the Holocene has been dramatically dominated and altered by humans, and we are now in the era of the 'Anthropocene' (Steffen et al. 2011). Climate change over the last two decades has been occurring at a rapid rate and scale (Walther et al. 2002), and this poses a major question: will organisms be able to adapt fast enough? Over 50% of the Earth's land surface and atmosphere has been modified by human activity, with associated environmental changes such as habitat alteration, emission of greenhouse gasses and deposition of organic and plastic pollutants. Among the various anthropogenically induced changes in the environment, urbanisation is the most dramatic. Urbanisation modifies natural ecosystems almost completely and introduces novel challenges for flora and fauna in the areas. Urbanisation not only replaces natural habitats with anthropogenic structures, such as roads and buildings (Sol et al. 2013), but also causes the loss, fragmentation, and alteration of the remaining natural habitats (Sol et al. 2013). In addition, urbanisation introduces pollution and toxicity to the environment (Sol et al., 2013). As a consequence of these structural changes to the environment, urbanisation affects ecosystems by changing the community of flora and fauna that survive (Sih et al. 2011; Sol et al. 2013). This altered community is further exposed to novel conditions, including humans, domestic animals, and other commensals (Fischer et al., 2012; Sol et al., 2013).

The whole new suite of environmental challenges, apart from climate change, that has emerged due to urbanisation poses a serious challenge for fauna and flora. These changes which are unique to the evolutionary history of the affected species have been termed "human-induced rapid environmental change" (HIREC, Sih et al. 2011). Urban ecosystems differ from non-urban (rural or unmodified) ecosystems in several

The Urban Heat Island Effect

Climatic characteristics of cities are different from natural or undisturbed habitats. The combination of the greenhouse effect and the high heat capacity of buildings and roads result in average air temperatures in cities that are 0.5 - 1.5°C warmer than normal for that region (Oke 2011; Phelan et al. 2015). Size, geographical location, and vegetation cover of the city directly influence the magnitude of the urban heat island effect (Oke 1973), with some the world's most populous cities, especially in the tropics, experiencing greater spatio-temporally variable heat intensities and temperature differences of as much as 12°C between urban and rural areas (Tran et al. 2006). In 2011, Peng et al. (2011) assessed the diurnal variation of surface urban heat island intensity (SUHII) across 419 large cities around the world. Urban heat is detectable and high, and these authors highlight the importance of vegetation in cities to mitigate urban heat (Peng et al. 2011). The urban heat island effect, in combination with global temperature rise poses a major physiological challenge for organisms, especially poikilotherms (Angilletta Jr and Angilletta 2009). In tropical environments, ecotherms are even more sensitive to increasing environmental temperatures (Tewksbury et al. 2008; Diamond et al. 2012), for they have evolved in thermal environments that have been relatively stable and thus have thermal tolerance ranges that are narrower than organisms in temperate areas (Sunday et al. 2012). Ectothermic poikilotherms in tropical environments also live closer to their upper thermal limit, which gives them little flexibility to tolerate even higher temperatures (Deutsch et al. 2008).

ecologically relevant ways. Biotic and abiotic changes in urban environments include microhabitat characteristics, food availability, predation pressure, population density and human disturbance, which collectively alter trophic interactions but also the context of those interactions. Species residing in urban environments are now facing these multiple levels of challenges, and for some species, urbanisation relaxes selection pressures, but for others, HIRECs increase the pressure. The impacts of climate change are therefore heightened in urban ecosystems as other anthropogenic disturbances add to the already growing list of novel selection pressures (Figure 1).

Individuals can respond to these environmental challenges in three different ways: spatially, temporally, and by altering traits (Bellard et al. 2012). Firstly, species that are able to track environmental conditions in space can disperse to new microhabitats with suitable climatic conditions. Secondly, as an effect of changing temporal cycles of temperature and precipitation, species can also shift various life cycle events accordingly. For example, flowering patterns have advanced more than 10 days per decade in some species of plants (Parmesan 2006). Lastly, species can cope with the changing climatic conditions by altering several traits such as behaviour, physiology, morphology and life history. However, there are two fundamentally different kinds of trait shifts, depending on whether changes are predictable or unpredictable. In anticipation of predictable changes in the environment, organisms actively modulate their morphology, physiology and behaviour to cope. When faced with unpredictable events, organisms rapidly respond with facultative changes in behaviour and physiology during or after the event. Thus, questions such as how dispersal capabilities and even plasticity or microevolutionary changes in traits enable the continued presence of native taxa in urban environments become relevant. For the rest of this chapter, we organize our understanding of organismal responses to environmental disturbances in urban areas into two broad categories: 1) changes in community structure or biodiversity and 2) changes in species traits (Figure 1).

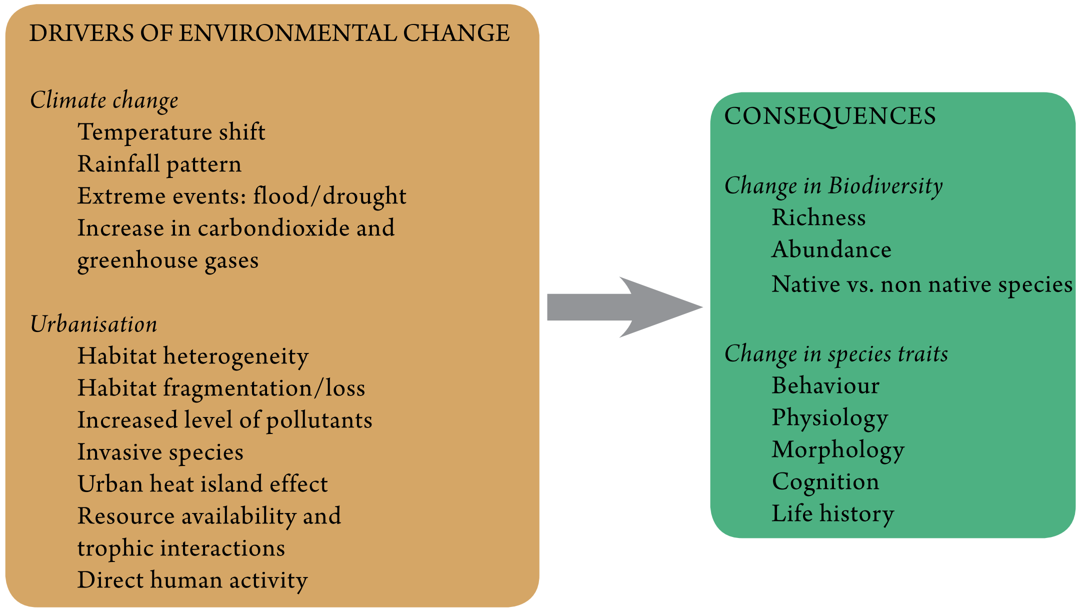

Figure 1. Illustration of some common drivers of environmental change due to climate change and urbanisation, and the consequences to communities and species.

CHANGE IN COMMUNITY STRUCTURE

Species Richness

Changes in species richness and abundance have been extensively documented across the urban-to-rural gradient in a wide range of taxa. But the patterns and extent of these shifts in species diversity depend on the taxa and type of urbanisation. For birds, beetles, butterflies, lichens and some groups of plants, we have considerable evidence that species richness typically decreases along the gradient from rural to urban (Seaward 1982; Blair 1999; Marzluff 2001; Lim and Sodhi 2004; Paul and Nagendra 2015). For most of these taxonomic groups, habitat loss is the primary cause of species loss. Habitat fragmentation of the remaining natural habitats in urban areas further affects species richness, especially for those that depend on large habitat patches, such as some birds and large mammals (Clergeau et al. 2006; McKinney 2008). Notably, fragmentation can also negatively affect species with low dispersal ability, such as carabid beetles (Niemelä and Kotze 2009; Goddard et al. 2010; Evans et al. 2009b). For Mediterranean butterflies, current trends in global climate change and the lack of patch connectivity in urban environments are projected to greatly reduce species assemblages (Stefanescu et al. 2004).

Even within taxonomic groups, the relationship between urbanisation and species abundance shows considerable variation. For example, Lim and Sodhi (2004) found that different avian resource guilds respond in different ways in a tropical urban environment. Insectivore and omnivore guilds of birds decreased in the number of species and abundance of species in urban habitats but the granivorous birds increased in abundance with urbanisation. These patterns illustrate the importance of resource availability for these taxa. Although urbanisation reduces insect abundance, thereby affecting insectivore guilds, some birds such as the rock pigeon or tree sparrows which are mainly granivorous can effectively exploit alternative and abundant anthropogenic food sources. Species abundances of frugivorous birds also depend on the extent of urban development and the resulting availability of food sources; a pattern observed in several studies (e.g. Reichard et al. 2001; Lim and Sodhi 2004).

Along with increasing temperature and habitat fragmentation, unprecedented growth in urbanisation will also bring major hydrological challenges, especially in the form of low water availability for wildlife. The rate of human population growth compounded by global climate change is expected to result in frequent drying of natural water resources or low water levels in freshwater systems, especially in urban environments when water is needed for human use as well as wildlife. The major taxa which will be affected are undoubtedly freshwater endemic fishes and water birds, as has been already observed in some cities around the world. More than 50% of the endemic fish in the Mediterranean Basin are categorised as 'vulnerable' or 'endangered' and anthropogenic development is exacerbating the situation (Smith et al. 2006). This issue is of major importance for the Western Ghats in India where there is high endemic fish diversity and a rapid increase in anthropogenic development, including urbanisation.

However, other groups of taxa, such as arthropods, are able to exploit and thrive equally well in urban as well as wild habitats (Sattler et al. 2010). This can be a result of heat island effects in urban areas and also spatial proximity of heterogeneous microhabitats that might meet the various requirements of the different life-cycle stages of arthropods.

A completely different relationship between urbanisation and species richness has been found for vascular plant species in North America and Europe. Plant species richness is often higher in cities compared to surrounding rural areas (McKinney 2002; Kühn et al. 2004; Wania et al. 2006; Knapp et al. 2009; Hope et al. 2008). This increase in richness of flora in cities seems to be a result of: (1) habitat heterogeneity within urban areas, which supports the different habitat requirements for multiple species and the (2) introduction of exotic species by humans which also have higher tolerance (McKinney 2002; Kowarik 2011).

However, detailed studies from the Indian subcontinent show that vegetation is not well-distributed in several Indian cities such as Delhi, Bangalore and Mumbai, where the core city area or the older parts of the city have high vegetation cover compared to the peripheral areas with newer anthropogenic development that are low in native vegetation (Nagendra et al. 2012; Paul and Nagendra 2015). As urbanisation rapidly extends to the periphery of the city, it is important to understand the serious implications for the sustainability of cities, which includes the importance of maintaining well-connected green spaces rather than fragmented ones. In addition to vegetation composition, species diversity of native fauna needs to be seriously considered while planning smart cities in India.

Native vs. Non-Native Species

In over 50 years, the diversity of vascular plant species in Belgium had not changed significantly but about 9% of the native species (N=58) were lost and replaced by 57 exotic species (Godefroid 2001). This kind of trend has been observed across the globe, and is a cause for major concern because of the disruption in the functional relationships between flora and fauna. For example, Khera et al. (2009) found a negative impact of non-native woody vegetation species on the species richness of birds in Delhi, India. However, in spite of highly altered urban landscapes across the world, species diversity across several taxa are not significantly affected, and the major reason behind this pattern is that native species have been replaced by exotics.

Rock pigeon (Columba livia), Thimpu, Bhutan (Photo: Qazi Faizul Hasan)

Multiple studies in plants have revealed lower phylogenetic diversity in urban areas where only some species-rich lineages benefit - such as plants with succulent or scleromorphic leaves that are well adapted to tolerate warm and dry city conditions (Knapp et al. 2008a, b, 2009). Thus, some species actually benefit from the climate and environmental conditions in urban areas (defined as 'urban exploiters' or 'urban specialists' by Blair (2001); Hill et al. (2002)). A few studies also have demonstrated that the dry and warm climatic conditions in urban areas are one of the major causes for survival and proliferation of some exotic species, such as *Ailanthus altissima*, which is a native of China, but is now also found in the urban centres in central Europe (Kowarik and Säumel 2007). Generalist species with higher tolerance ranges, greater phenotypic plasticity and behavioural flexibility are able to adapt to changing urban environments while native specialists or endemics are at major risk all across the globe. For example, presence of brown anoles (*Anolis sagrei*), a non-native species, has negative impacts on the abundance of crested anoles (*Anolis cristatellus*), a native species in some Caribbean cities. (Kolbe et al. 2016). Invasive species and household pets can also act as novel predators or parasites for a large number of local fauna (Cox and Lima 2006; Sih et al. 2010; French et al. 2018).

Our understanding of the effects of global climate change and urbanisation on overall biodiversity loss and associated species responses are still being modified with the rapid addition of new studies. Several predictive models quantitatively show high rates of biodiversity loss (Thomas et al. 2004; Soberón and Nakamura 2009; Sinclair et al. 2010), but these modelling approaches largely focus on one axis of change – change in habitats and associated changes in species persistence and abundances across space. Although there is a lot of variation in the different modelling approaches for predicting biodiversity loss, a general conclusion from all models is a loss of species across multiple taxa at the global scale (Bellard et al. 2012). However, organisms are capable of adjusting to change and thus, a mechanistic understanding of species responses are equally important aspects that should be incorporated in future models.

Change in Species Traits

Human-induced rapid environmental change (HIREC) has exposed organisms to novel challenges and conditions which they have not experienced in their recent past (Sih et al. 2011). As a result of HIREC, species interaction in the environment is altered and this leads to species declines, range shifts and adaptive evolutionary responses. On one hand, the majority of studies report and predict species declines in the near future, but there are some species which are thriving in urban areas (such as invasive species and urban exploiters). Even in the same taxa or genus, we find species at the two extremes (Rehage and Sih 2004; Rehage et al. 2005; D'Amore et al. 2010). Thus, it is important to understand the mechanism of how and why some species are faring better than others when faced with HIREC. With the understanding that explains and ideally predicts the outcomes of how individuals or species will respond to global climate change and urban disturbances, important management plans to control species decline or pest infestation can be addressed.

*House sparrow (*Passer domesticus*) using man made box (Photo: Rohan Chakravarty)*

Behaviour

Changes in biotic and abiotic conditions of the environment due to rapid human-induced disturbances can cause shifts in the behaviour of animals. Behavioural shifts can either be adaptive to the new conditions or maladaptive, which might then lead to fitness losses and a decline in species abundance. Behavioural changes seen in urban populations of animals include alterations to foraging, microhabitat use, dispersal, anti-predator, social and reproductive behaviour. For example, high anthropogenic disturbances in terms of human mobility and vehicular traffic can disrupt foraging efficiency in several animals which tend to avoid human activity, or shift their foraging time to after dark when human activity is comparatively lower (Tigas et al. 2002; Dowding et al. 2010). Conversely, greater food availability in urban areas due to human food provisioning and resource shift have also resulted in unexpected alterations in the diet of urban residents, as well as associated behaviours like early breeding or lower foraging activity (Lowry et al. 2013; Balakrishna et al. 2016).

Apart from exploiting urban resources for food, animals also use anthropogenic structures as refuges. Many species of small mammals (e.g. possums (*Trichosurus vulpecula kerr*), chipmunks (*Tamias striatus*), stone martens (*Martes foina*), squirrels (*Sciurus niger*)) and reptiles (e.g. Indian rock agama (*Psammophilus dorsalis*), blue tongued lizard (*Tiliqua scincoides*)) use artificial structures as shelter against predators or as dens (Ryan and Larson 1976; Statham and Statham 1997; McCleery et al. 2007; Herr et al. 2010; Batabyal et al. 2017). Increased tolerance to urbanisation is observed in several species, where individuals decrease risk perception to anthropogenic stimuli (Tuomainen and Candolin 2011; French et al. 2018). Notably, organisms can tolerate only up to a certain level of disturbance, as is observed in the urban house sparrows (*Passer domesticus*), wherein they are present in areas with intermediate pedestrian traffic when they can effectively utilize anthropogenic food sources, but their foraging and breeding activity decreases as traffic level increases (Fernández-Juricic et al. 2003). Apart from being tolerant, being bold in temperament allows wildlife undergoing synurbanisation (the process of be becoming urbanised) to live in close association with humans (Warne and Jones 2003; Ross 2004; Garden et al. 2006; Lowry et al. 2011).Urbanisation creates a number of disturbances in the sensory environment of animals in the form of altered light conditions and increasing noise and chemical pollution. Since behavioural responses of individuals depend on the information they acquire from their surroundings, the disruption in the sensory environment has major effects on animal communication and subsequently, fitness. Humans influence the visual environment by modifying the duration and quality of light and also by changing visibility. These conditions highly alter activity patterns across a range of animal groups - especially nocturnal animals - as they are attracted towards artificial bright lights that end up disrupting their natural visual cues for communication and navigation. Because nocturnal insects are attracted to light, many insectivorous birds, frogs, reptiles and bats are attracted towards bright buildings and road lights at night, which disturbs their natural foraging regimes (Longcore and Rich 2004; Thums et al. 2016).

Artificial lighting also affects marine organisms such as the hatchlings of green turtles (*Chelonia mydas*) which are attracted towards shore lighting, in turn exposing them to greater risk of predation (Thums et al. 2016). Disturbed visual environments such as turbid water caused by eutrophication severely affect animal communication and can even cause mortality from hypoxia or infection. For example, in several fish species, water turbidity leads to altered mate choices (Seehausen et al. 1997; Candolin et al. 2007; Wong et al. 2007; Maan et al. 2010), and in birds and amphibians, artificial lighting leads to temporal shift in advertisement calls (Miller 2006; Baker and Richardson 2006).

Acoustic communication in animals is also affected by constant, low-level anthropogenic noise. Animals generally adjust their acoustic signals by altering frequency of calls as is observed in many urban dwelling bird species (e.g. great tits, European black birds, noisy miner) which sing at higher minimum frequencies compared to their rural counterparts (Lowry et al. 2013). Several animals also depend on olfactory cues for communication, and the spread of urban pollutants and pesticides highly alter mate choice in these animals by disrupting pheromonal signals (Lürling and Scheffer 2007). Thus, differences in behaviour of urban and rural conspecifics across taxa are wide-ranging, with repeated evidence for urban individuals being higher in risk taking (bolder), aggression, exploration, and neophilia compared to their rural counterparts. However, whenever

Termites over a lamppost (Photo: Nikhil Pradip More) documented, communication is majorly affected in urban environments.

Cognition

Learning in response to new stimuli enhances the ability of animals to adjust to novel environmental conditions. Urban landscapes and the presence of humans are not always perceived as threats by animals, but the ability to learn what is and is not a threat is beneficial. Studies on anti-predatory behaviour show the importance of habituation in influencing escape responses in birds and reptiles. Urban birds appear to be generally less wary than rural birds (Lowry et al. 2011) and similarly, lizards in urban areas allow closer approaches before escaping (Batabyal et al. 2017). For these taxa, reduced wariness was a learned response; individuals became habituated to anthropogenic disturbances. Experiments have shown that pigeons and magpies are able to recognise humans who provide them food (Belguermi et al. 2011) and also display reduced aggression towards humans that do not pose a threat to their nest (Lee et al. 2011). Several such studies have been performed with avian species, and these demonstrate enhanced learning skills in urban birds compared to non-urban ones (Roth and Pravosudov 2009; Pravosudov and Smulders 2010; Sol et al. 2011; Freas et al. 2012). The unpredictability and complexity of the environment have been hypothesised to increase cognitive skills across other taxa, such as in fish (Mackney and Hughes 1995; Brydges et al. 2008), mammals (Barton and Harvey 2000), and reptiles (Batabyal and Thaker, forthcoming). Larger brain size and innovation in feeding behaviour have been suggested as key for urban dwellers to successfully thrive in these altered landscapes (Maklakov et al. 2011). Thus, behavioural flexibility and learning skills are common in animals and might allow species to adjust to rapid changes in urban environments.

Physiology

Humans activity and the direct and indirect alterations to the environment influence behaviour of animals through physiological processes. Major physiological pathways which are affected due to anthropogenic disturbances are neuro-hormonal and immune responses. Increased temperature due to global climate change leads to major challenges for thermoregulating ectotherms in terms of maintaining cooler body temperatures in the heat. Thermal tolerances of poikilothermic species can vary across geographical range and can evolve to adapt (Marsh 1985; Clémencet et al. 2010; Oberg et al. 2012; Verble-Pearson et al. 2015). For example, ants can evolve their thermal tolerance within a few generations in response to increased temperatures (Diamond et al. 2017), which may explain why some ant species show variation in thermal tolerances across the rural-urban gradient. An urban population of leaf-cutter ants from Brazil show higher heat tolerances than their rural counterparts, which might be beneficial during high activity, as the urban trails used by ants heat up significantly during the day (Angilletta et al. 2007). Most ectotherms behaviourally thermoregulate, by shuttling between shade and sun to maintain their preferred temperature. Urbanisation and global climate change have together resulted in a reduction in vegetation cover, and thus, availability of thermal refuges (i.e. shade) is considerably limited. Ectotherms thus face a major challenge in terms of altering their activity patterns and seasonal breeding cycles, depending on the increasing temperature and availability of vegetation cover or shade (Huey and Tewksbury 2009; Kearney et al. 2009). Some have suggested that with global warming, temperatures will be too high for ectotherms to be active, and this prolonged need to seek thermal refuges may actually result in lower fitness and a reduction in species survival (Sinervo et al. 2010).

Another common physiological pathway that is affected by urbanisation is stress responses, mediated by the activation of the hypothalamo-pituitary-adrenal axis which finally leads to a release of glucocorticoid hormones. Glucocorticoids are necessary to maintain homeostatic processes of glucose mobilisation, but are also essential for stimulatory, suppressive and preparative responses of animals to additional stressors (Sapolsky et al. 2000). Comparison between urban and rural individuals of species across taxa show a mixed response for glucocorticoid levels. For example, in males of the European blackbird (*Turdus merula*) and white-crowned sparrow (*Zonotrichia leucophrys*), baseline plasma glucocorticoid levels are lower in urban populations compared to rural populations (Partecke et al. 2006; Bonier et al. 2007), whereas stress-induced glucocorticoid levels in Florida scrub jays (*Aphelocoma coerulescens*, Schoech et al. 2004) and circulating levels in the northern mockingbird (*Mimus polyglottos*) and curve-billed thrasher (*Toxostoma curvirostre*) are higher in urban populations than rural populations (Fokidis et al. 2009). Similar mixed responses are also found in reptile species (French et al. 2018). Hence, stress responses in urban residents are not only species-specific, but are also highly variable. This is not surprising, as stress responses depend on several factors, such as the timing of colonization or urbanisation, specific stress factors in the urban habitat such as food resources and predators, and the life history stage and other associated functional traits of the species involved. Stress response pathways also have a direct effect on the immunity of animals as glucocorticoid receptors are present on the lymphatic tissues and leucocytes throughout the body. But the specific relationship between stress and immunity varies across context; chronic stress responses typically lead to immunosuppression but acute stress enhances immunity (Dhabhar and McEwen 1997; Dhabhar 1998, 2000, French et al. 2008, 2010). Recently, Amdekar et al. (2018) showed that health and immunity measures can be used to determine how well species are physiologically coping to urbanisation. In birds, urban adaptors and urban exploiters differ in key physiological

Psammophilus dorsalis *(Indian rock agama), Bangalore (Photo: Anuradha Batabyal)* ways that reflect their ability to modulate their health (Isaksson et al. 2017). Studies during the past decade have also found an increase in the prevalence of disease in urban habitats. The overlap between high densities of multiple host species, such as feral and domestic felids and urban bird species allow for increased disease transmission, especially of bacteria and virus forms that infect wildlife (Brearley et al. 2013).

However, similar to stress response, mixed patterns have been found for disease prevalence. For example, blood parasite infections in blackbirds and tapeworm infections in red foxes were found to be lower in urban habitats because the appropriate vectors were less abundant (Brearley et al. 2013). Thus, the effects of human-modified environments on health and stress physiology in animals needs to be better understood as it is a potential driver that affects the variation in survivorship and persistence that we observe across taxa.

Morphology

Urban areas have distinctive selection pressures that are different from surrounding rural areas, and this might lead to morphological trait divergence in urban populations. Interestingly, in some species (e.g. common wall lizards), certain aspects of morphology are found to show higher fluctuating asymmetry in urban environments, while in other species (ground beetles) no difference in asymmetry is observed (Lazić et al. 2013, 2015; Elek et al. 2014). Other morphological traits such as limb length and body condition also tend to show mixed patterns depending on urban habitat structure and resource abundance (Evans et al. 2009a). Limb morphology especially seems to be modified to suit particular microhabitat conditions which facilitate quicker movement (French et al. 2018).

Similar to animals, plant morphological traits also show variation across urban and rural areas. A review of 29 plant studies shows that some traits, such as woodiness, height and seed mass, have an increasing trend in urban areas, while other functional traits showed mixed responses (Williams et al. 2015). Variation in the patterns of trait shifts is dependent on the consistency and strength of local selection pressures that act on those traits. Notably, shifts across multiple traits might have long-term consequences on fitness and could also potentially lead to evolutionary divergence.

Life History

Life history characteristics and degree of habitat specialization in animals influence how they respond under changing environmental conditions. Life history majorly governs behavioural responses in animals because it ascertains allocation of resources to current or future needs. For instance, animals facing a current disturbance can choose to stay or leave that area and potentially forego the value of current offspring to future reproductive opportunities. The outcome of such choices would differ across species depending on lifespan, generation time, and habitat specialisation. Generalist species which are typically less sensitive to anthropogenic disturbance often have better chances of survival as they can utilize human-modified landscape changes in their favour. For example, in south-east England, common frogs better survived urbanisation while common toads could not, because frogs were able to use urban ponds to lay eggs better than toads (Carrier and Beebee 2003). Animals select suitable habitat based on several environmental cues. However, HIRECs often modify these cues, such that they become less informative or even incorrect. As a result, urban environments can become ecological traps with active selection of urban habitats despite the lower fitness outcome (e.g. Battin 2004). The major long-term consequence of ecological traps is local extinction of species (Hale and Stephen 2016).

Many species also require multiple distinct habitats to complete their life cycle, and therefore, degradation in any one of the habitats might lead to population decline. Apart from altering terrestrial ecosystems, urbanisation majorly affects aquatic environments. This causes a severe loss of habitat for spawning, for a variety of amphibians and fish species - for example, salmon (*Oncorhynchus nerka*) and common galaxias (*Galaxias maculatus*) which need specific aquatic conditions for egg survival (Nehlsen et al. 1991; Hickford and Schiel 2011). There have also been some unintended benefits of urbanisation on life history characteristics of urban residents. In temperate regions, some plants now have longer growing seasons in urban areas due to increased temperature and the heat island effects of cities (White et al. 2002; Lu et al. 2006; Neil et al. 2010). Thus, it is important to consider the natural life history conditions of existing wildlife in urbanised landscapes to design specific conservation management programmes, such that life stage-specific habitats which are required for completion of life cycle for several organisms are not degraded.

CONCLUSION

We are still far from understanding how climate change and associated anthropogenic disturbances are impacting species and ecosystems. However, there is no doubt that several phenotypic traits (behaviour, cognition, physiology, morphology, life history) of species are exhibiting major shifts due to novel selection pressures. These trait shifts in turn can affect survival and reproductive success of individuals, which can influence abundance, species richness and distribution range in disturbed areas. Considerable evidence has shown that a limited set of species that are tolerant and show greater flexibility are able to thrive in highly urbanised environments.

Although a lot of research is being carried out to record the phenotypic changes to species (populations) as a function of changing climatic conditions, we still lack an understanding of the mechanisms behind these responses or the fitness consequences. Those are the levels that will allow us to understand and even predict the evolutionary impact of functional trait changes. To be able to persist in the face of climate change and urban disturbances, individuals, populations, or species which can produce adaptive responses through plasticity or microevolution have increased chances of survival. The step forward is to gain a more comprehensive overview of all these factors which can substantially improve our predictive power of the fate of species facing global climatic challenges, and also help in effective conservation management plans.


Cattle egret (Bubulcus ibis)
(Photo: Nikhil Pradip More)

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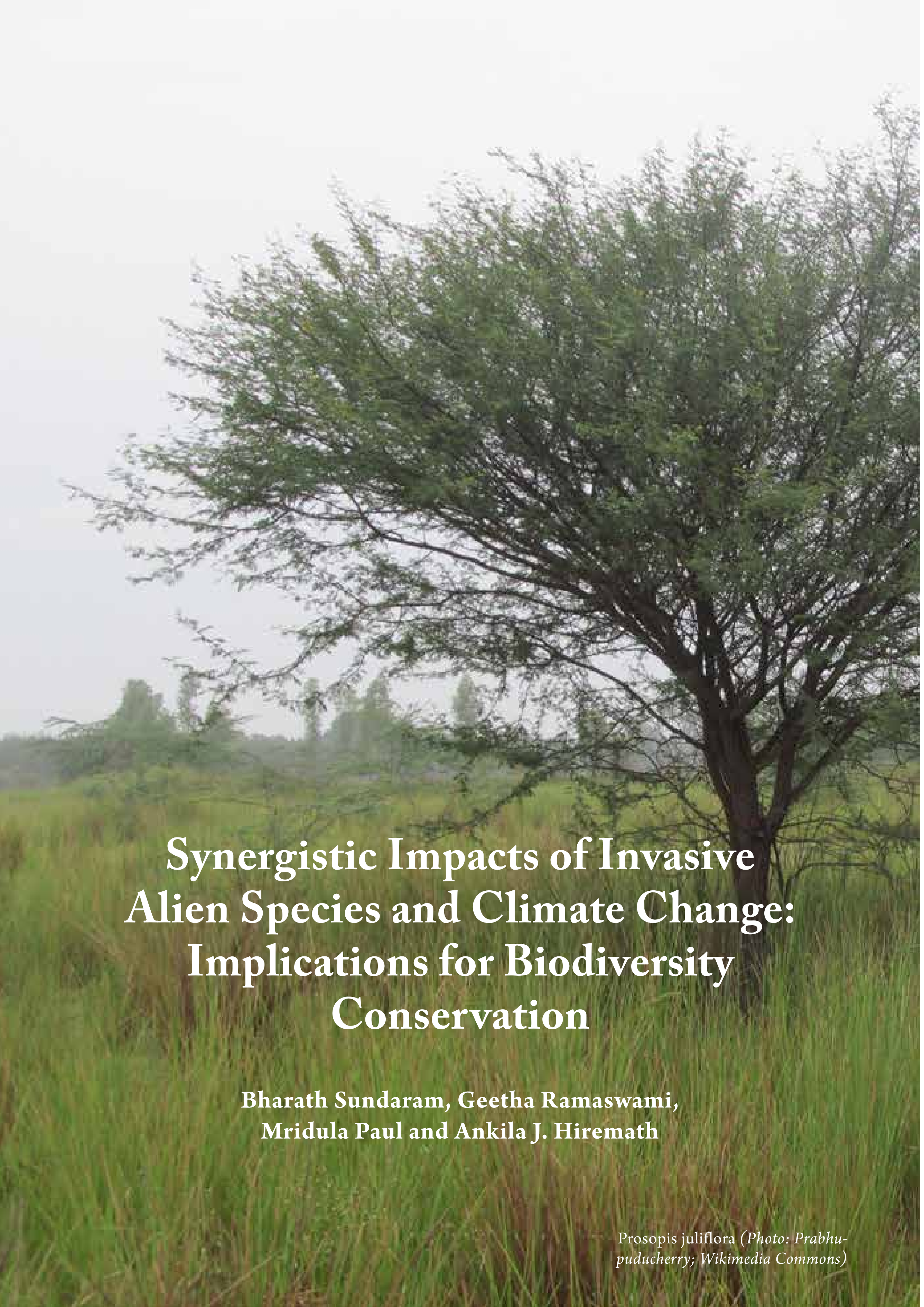

Synergistic Impacts of Invasive Alien Species and Climate Change: Implications for Biodiversity Conservation

Bharath Sundaram, Geetha Ramaswami, Mridula Paul and Ankila J. Hiremath

Prosopis juliflora *(Photo: Prabhupuducherry; Wikimedia Commons)*

> *"Someday, perhaps not long from now, the inhabitants of a hotter, more dangerous and biologically diminished planet than the one on which I lived may wonder what you and I were thinking, or whether we thought at all……"*
>
> *Vollman 2018, No Immediate Danger, Vol. 1 of Carbon Ideologies*

INTRODUCTION

Climate change and invasive alien species are considered to be primary threats to biodiversity and ecosystem functioning globally (Vitousek et al. 1997; Steffen et al. 2015; Tilman et al. 2017). It is estimated that 25% of all mammal species, 13% of all bird species, and over 21000 species of plants face a high probability of extinction within a 50-year window (Tilman et al. 2017). In addition to climate change and invasive species, threats to biodiversity come from unsustainable resource consumption and extraction, land use and land cover change, and pollution. While each of the factors listed above are potent enough when viewed individually, additional challenges to conserving biodiversity and ecosystems come from the threats posed by the interaction among them.
In this chapter, we explore and examine different facets of how climate change and alien invasive species interactively threaten biodiversity in India.

We review how Indian ecosystems are likely to change with changing climate (e.g. Rasquinha and Sankaran 2016). We then describe how alien invasive species are likely to respond to various climate- and ecosystem-change scenarios (e.g. Adhikari et al. 2015; Panda et al. 2018). These responses of invasive species include the potential influence of climate change on the various aspects of the invasion pathway (Hellmann et al. 2008; Leishman and Gallagher 2015), as well as how climate change is likely to exacerbate already existing impacts of alien invasive species on human well-being. We then explicate India's policy position on invasive species as a signatory to international agreements pertaining to the various ecological and social impacts of alien invasive species and climate change. We end by presenting a range of possible management responses towards addressing alien invasive species in a changing climate, and point out research, policy, and management gaps for further work. Our review is not meant to be a comprehensive literature review of alien invasive species research in India, and we refer largely to material pertaining to plant invasive species in terrestrial ecosystems.

PROJECTED ECOSYSTEM CHANGE UNDER DIFFERENT CLIMATE CHANGE SCENARIOS IN INDIA - PATTERNS AND UNCERTAINTY OF ECOSYSTEM CHANGE AND SUSTAINABILITY FOR ALIEN INVASIVE SPECIES

Climate change is likely to bring about a number of changes in the structure and functioning of ecosystems. Terrestrial and aquatic ecosystem properties that are likely to be affected by increasing atmospheric CO_2 and global temperatures include changes in ecosystem productivity, biogeochemical cycles and carbon dynamics, altered disturbance regimes, and altered food chains and food webs (e.g. Petchey et al. 1999; Wrona et al. 2006; Grimm et al. 2013). In terrestrial ecosystems, the net ecosystem productivity under most climate change scenarios has been predicted to increase in the early part of the 21st century, but will subsequently stabilise and eventually reduce (Cramer et al. 2001). In peat-land ecosystems, variability in community composition (including shift to predominantly vascular plants from predominantly non-vascular plants), and soil properties such as pH are likely to increase (Dieleman et al. 2015). Ecosystem perturbations may benefit invasive species that possess the physio-logical capability to deal with the ecosystem-level consequences of climate change. Invasive species are considered to be a part of global change, and act synergistically with climate change and other anthropogenic changes such as habitat fragmentation (e.g. Kuczynski et al. 2018). Indeed, it is often not clear whether invasive species are driving ecosystem and community change, or benefiting from changes to ecosystems and communities (Macdougall and Turkington 2005).

In India, the patterns of ecosystem change under future climate are poorly understand – much less their impacts on invasive species. Under future climate change scenarios, biomes of the Indian sub-continent are set to shift from their current state to a different state. For example, 14-18% of India is set to experience biome shifts—from dry to wet in certain areas and vice-versa in others, with dry and xeric habitats being under high risk of change (Ravindranath et al. 2006; Chakraborty et al. 2013; Rasquinha and Sankaran 2016). In the Himalayas, the impacts of climate change have been predicted to affect amount and seasonality of precipitation, recession of glaciers, alterations in plant phenology with cascading effects on pollinators, species interactions, local extinctions, latitudinal and altitudinal shifting of tree lines, and large-scale changes in montane grassland ecosystems (Xu et al. 2009). Climate change may also alter the characteristics of the predominant vegetation. For instance, historically, in montane habitats of India, cool, dry, low-CO_2 periods were associated with the dominance of C4 physiological strategies like those of grasses, while warmer, wetter periods were associated with the C3 physiological strategies characteristic of most woody plants (Sukumar et al. 1995). With future warming too – especially with increasing atmospheric carbon dioxide – one can expect a proliferation of these physiological strategies common in many woody, exotic and weedy plants, such as Australian wattles (*Acacia* spp., Sukumar et al. 1995).

One way of understanding the responses of invasive species to future climate change is through species distribution modelling, based on the principle of predicting potential niches of species using their current geographic spread (e.g. Thuiller et al. 2005; Barbet-Massin et al. 2018). Species distribution modelling of invasive plants, under climate change or otherwise, is a tricky endeavour. Predicted species' ranges that are often based on environmental proxies, do not always account for different responses to environmental factors in their realised and novel niches. For instance, species often occupy a more variable range of environmental parameters in their novel ranges than in their native ranges (Hierro et al. 2005; Broennimann and Guisan 2008). Thus, species range predictions are likely to be affected by whether a model was trained using the invasive plant's native range or introduced range, and pooling distribution information from both ranges may yield better predictions for species spread (Broennimann and Guisan 2008; Mainali et al. 2015). Predicted ranges may also be under-representations, as invasive species have not had as much time as native species to attain maximum range expansion (Bradley et al. 2015). Studies from across the globe have also predicted the effect of climate change on the spread of invasive species. Responses to climate change in terms of range expansions are likely to be species-specific, with some invasive species' ranges increasing, while others reduce within the same kinds of habitats (e.g. Merow et al. 2017).

In India, species range predictions have been made through ecological niche modelling techniques coupled with future climate change scenarios. One such study has found 49% of the geographical area of India to be susceptible to invasion by exotic species, and that 19 out of 47 ecoregions of India harboured invasion 'hotspots' often coinciding with ecologically valuable regions (Adhikari et al. 2015). Other studies have modelled range expansions for individual species such as *Lantana camara*, *Cassia tora and Sapium sebiferum* (Bhagwat et al. 2012; Jaryan et al. 2013; Panda et al. 2018). For instance, both *L. camara* and *C. tora* are predicted to spread to newer areas across India as more habitats become suitable for expansion, owing to changes in temperature and precipitation under future climate change scenarios (Panda et al. 2018).

Species range expansions have also been addressed at more regional scales. In the Himalayas, some species such as *Ageratum conyzoides* and *Parthenium hysterophorus* are likely to lose suitable habitat by the latter half of the 21st century, while others such as *Ageratina adenophora, Chromolaena odorata*, and *L. camara* are predicted to gain suitable habitats for further invasion (Lamsal et al. 2018). At more local scales too, such as in the Kailash region of the Western Himalayas, as many as 11 invasive alien plant species are predicted to spread further than their current distributions by the latter half of the 21st century (Thapa et al. 2018).


Acacia auriculiformis *(Photo: Scamperdale; Flickr)*

PREDICTING THE IMPACT OF CLIMATE CHANGE ON THE INVASION PATHWAY: THEORETICAL GUIDANCE

Theoharides and Dukes (2007) reviewed how climate change is likely to affect the four stages of the invasion 'pathway': (1) transport, (2) colonisation, (3) establishment, and (4) landscape spread. A species must typically pass through a variety of environmental filters at each of these stages before it be-comes invasive (Theoharides and Dukes 2007; Hellmann et al. 2008). Climate change can potentially impact each of these stages in different ways.

Transport requires the intercontinental movement of species, either naturally or because of human intervention. The rates at which species are transported across biogeographic zones has increased in intensity due to the rapid proliferation of trade networks (Seebens et al. 2015). Due to the expansion of existing trading networks (market expansion), the creation of new networks (market creation), and the increased transport of biologically active products through cold chains, species are now being transported over much longer distances, and in a biological state that render them more capable of progressing to the next stages. Three categories of plants – horticultural species, crops, and plants cultivated as biofuels – pose specific problems due to their rapid movement across the globe. Khoury and Achicanoy (2016) describe how globally, most countries are now highly interconnected with regard to the primary regions of diversity of crops they cultivate and consume, with 69% of national food grown being foreign in origin. The implications of these findings are twofold. Firstly, the rate of species transport is likely to increase as potential invasive species piggyback on trade networks that have evolved to transport seeds of commercially grown species to distant markets for production or consumption. Secondly, given that food-insecure regions, such as South Asia and Southern Africa, are predicted to become less climate resilient over time (Lobell et al. 2016), the transport of food crops (and the non-native species that accompany them) is only likely to increase. Once species have successfully been transported outside of their original environment, they are exposed to a different set of environmental conditions (climate, hydrology), in addition to biotic exposure to a different set of autotrophs, heterotrophs, and detritivores. Success in adaptation to these new abiotic and biotic conditions enable them to settle into the second stage of the invasion process: colonisation. Sakai et al. (2001) describe how arriving populations must survive and achieve positive growth rates despite their low density, and be able to tide over demographic stochasticity and lack of genetic variability. This implies that only a fraction of species that are transported are likely to successfully colonise a new area, with some researchers estimating that only 10% of all species that are transported are likely to successfully naturalise in areas outside of their origin (Williamson and Fitter 1996). Due to their high phenotypic plasticity, high capacity for hybridization, and broad environmental tolerance, the likelihood of successful colonisation of species that have survived the transport stage will possibly increase with climate change (Theoharides and Dukes 2007). Moreover, with climate change, species that are currently unsuccessful may find conditions changed to facilitate successful colonisation. Because of their capacity for rapid reproduction, and their enhanced nutrient use efficiency, non-native species that are lying in wait may find conditions that favour colonisation, and may therefore progress further along the invasion pathway.

Once a species has successfully colonised an area, its capacity to develop self-sustaining and expanding populations determines its establishment, which is the third stage in the invasion pathway. At this stage, small subpopulations of individuals may be linked through dispersal, and may come out as winners in ecosystems where they either face reduced competition from native species, or represent functional groups either absent, or present in low abundance, within the community (Melbourne et al. 2007), thereby giving coloniser species an edge over native species. At this stage, habitat heterogeneity and the availability of empty niche space also play a role in cementing establishment. Climate change is likely to cause climatic range restrictions and expansions of native and non-native species. Qian and Ricklefs (2006) likened this scenario of simultaneous constriction and expansion of range as a zero-sum game, where some non-native species that are habitat generalists are likely to benefit from range expansion, while those that are habitat specialists are likely to be negatively impacted by range constriction. However, in the long term, the shifting of climatic range restrictions is likely to tip the scales in favour of invasive species due to their broad environmental tolerances and high phenotypic plasticity (Sakai et al. 2001; Theoharides and Dukes 2007).

The final stage of the invasion pathway, landscape spread, is represented by invasive species forming a regional meta-community, where groups of populations are connected through long-distance dispersal (Melbourne et al. 2007). Within a heterogeneous landscape, populations of invasive species exist as interacting groups of species at different stages of colonisation and establishment. Theoharides and Dukes (2007) posit landscape spread as incorporating 'ideal' conditions from all three previous stages in the invasion pathway: regional spread rates of invasive species are influenced by landscape heterogeneity, the size, distribution, and availability of suitable habitat for colonisation and establishment, and population characteristics, growth rates, and dispersal ability of invasive species. Therefore, the final stage of the invasion pathway is a culmination of biotic and abiotic factors that enable landscape spread. Leishman and Gallagher (2015) suggest that the responses of native and alien species to changes in carbon dioxide, temperature, and rainfall will be strongly species and context dependent, so that alien invaders will not consistently be favoured. However, climate change is likely to reduce resilience of vegetation assemblages resulting in increased colonisation probability, presenting a window of opportunity that invasive species are best placed to take advantage of.

Impact of Alien Invasive Species and Climate Change on Human Well-being

Invasive species are increasing in number, extent, and influence worldwide (Pyšek and Richardson 2010). While the ecological impacts of invasive species have been generally well-studied, the many ways in which such species impact ecosystem services and human well-being are still emerging (Pejchar and Mooney 2009). In India, the effects of invasive species and climate change are likely to be iniquitously distributed and experienced, similar to patterns observed in poverty distribution. Over 270 million people in India have been classified to be living under the poverty line (World Bank 2012), and almost half of this number (43%) comprises the Scheduled Tribes (ST) and Scheduled Castes (SC), groups that are not only disproportionately dependent on natural resources for their livelihoods, but are also disproportionately poor in comparison with the rest of the Indian population. This constituency of people – with livelihoods directly dependent on forests or agriculture – is likely to disproportionately bear the brunt of altered provisioning services (food, fibre, fuel, and water) and regulating services (pollination, climate regulation, soil stabilisation, and flood mitigation) due to the effects of invasive species and climate change. In addition, cultural connects (religious belief, aesthetic value) that people share with the landscape that they live in are also likely to be impacted due to invasive species and climate change (Shackleton et al. 2018).

Reducing the adverse impacts of invasive species spread and climate change is made difficult due to two problems. First, information on changes in the status of invasive species, size of populations, and extent and condition of invaded habitat is patchy, with little or no data available for many ecosystems in India. Second, the impact of these changes on society is also poorly understood. Preparing for a climate-altered future is thus made extremely challenging.

Invasive species can be both drivers of ecological-community-change, or passengers that are taken along for the ecological ride (Macdougall and Turkington 2005) caused by other factors such as climate change. The potentially high climate cost of poverty alleviation measures in developing countries such as India, has the potential to further entrench the position of invasive species as both drivers and passengers of ecosystem change. The transformation in

Lantana invasion in BR Hills (Photo: Bharath Sundaram)

India's biophysical economy over the past 50 years, and the change in historical, current, and future demand for materials and energy seems to indicate that invasive species are likely to be both drivers of ecosystem change due to increased success met on the invasion pathway, and passengers that are helped along because of increased carbon dioxide emissions and a change in social metabolism. Singh et al. (2012) surmised that even though per capita resource consumption in India is still extremely modest, its sheer population and the challenges associated with poverty alleviation and providing a reasonable material standard of living poses sustainability challenges for the entire globe. For example, the annual domestic consumption of biomass (food, fibre, materials) doubled from around 1 gigaton in 1961 to 2 gigaton in 2008, the bulk of which was agricultural biomass. However, in the last three decades, the Indian economy has shifted from a biomass-intensive metabolic system towards a mineral- and fossil-resource-based society (Singh et al. 2012).

The larger implications of this for climate change is that raising the material living standards of the large majority of India's population will require greater intensity of access to energy and key mineral materials. Given the potentially high climate cost of India's current and future development, it remains to be seen as to how these costs are borne out by Indian ecosystems. Eventually, the carbon dioxide contribution of developing and fast-growing economies like India and China, and the resulting change in climate, is therefore likely to play a huge role in determining to what extent invasive species simultaneously become drivers and passengers of ecological change.

India's Policy Position on Alien Invasive Species

The international Convention on Biological Diversity (CBD), recognises invasive species as amongst the foremost threats to biodiversity. In its guiding principles on invasive species, CBD includes the prevention of their introduction, and their control and eradication, and emphasises research and monitoring, as well as education and awareness. As a signatory to the CBD, India has acknowledged the problem posed by invasive species in its biodiversity-related policy and planning process.

During the 11th national 5-year plan period (2007-2012), the centrally sponsored Integrated Forest Protection Scheme was relaunched as the Intensification of Forest Management Scheme; this new scheme included several additional components, one of which was the 'control and eradication of forest invasive species.' Further, the 12th national 5-year plan (2012-2017) proposed a national invasive species monitoring system.

India's National Biodiversity Action Plan (NBAP), which was drawn up in 2008 (MoEFCC 2008), listed a series of actionable steps relating to invasive alien species, to be achieved within a 5-year time frame. These included (1) developing a national database on invasive species; (2) developing an early warning and response system in response to new invasive species; (3) strengthening domestic quarantine measures to prevent further spread of invasive species; (4) supporting basic research on invasive species and capacity building to manage invasive species; (5) restoring landscapes degraded by invasive species; and (6) promoting regional cooperation on quarantine measures and containment of invasive species.

Several significant steps were taken in the aftermath of NBAP 2008. One of these was a national brainstorming meeting on invasive species that was held at Punjab University in 2009, under the aegis of the Ministry of Environment and Forests. The focus of the meeting was to evolve a coordinated national plan on managing invasive species, and it also resulted in an edited volume on invasive species (Bhatt et al. 2012). Another step was the setting up of a Forest Invasive Species Cell, under the Indian Council for Forest Research and Education, in 2009. The mandate of this cell included creating a database on invasive species and developing capacities for invasive species management.

Following the 2010 meeting of the Conference of Parties (CoP) to the CBD in Nagoya, the CBD adopted a new Strategic Plan for Biodiversity 2011-2020 and set a series of biodiversity targets, the Aichi Targets, to be achieved by 2020. In response, India brought out an Addendum to NBAP 2008 (MoEFCC 2014) and formulated a series of national biodiversity targets to be in synergy with the Aichi Targets. India's national target 4 (NBT4) on invasive species states, "By 2020, invasive alien species and pathways are identified and strategies to manage them developed so that populations of prioritised invasive alien species are managed." This corresponds closely with Aichi Target 9 ("By 2020, invasive alien species and pathways are identified and prioritised, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment.").

Policy vs. Reality

Despite the policy emphasis on invasive alien species, the reality concerning the status of invasive species management, research, and awareness in India is more sobering. Even a decade after steps to compile a database on invasive species, manage invasive species, and prevent further introduction and spread were outlined, there has been very little evidence of progress on the ground. One significant challenge in the context of invasive species is the lack of funds proportionate to the task. Just as an indication, in 2013-2014, the MoEFCC allocated Rs. 1824.14 crores towards biodiversity conservation under the 12 national biodiversity targets. National biodiversity target 4 (pertaining to invasive species) got Rs. 60.8 crores, a mere 3% of the total, and the second-lowest allocation. One possible explanation for this is that the Ministry of Environment, Forests and Climate Change is only one of the government agencies charged with the responsibility of meeting NBT4 – there are 25 other government ministries and departments besides, as listed in NBAP 2008 and NBAP 2008 Addendum 2014.

This dispersed responsibility was identified as a significant challenge to meeting the country's national biodiversity targets during a voluntary peer review to assess India's progress towards meeting the Aichi Targets, conducted by the CBD Secretariat in 2016 (MoEFCC 2016). (This voluntary peer review process was agreed to by CBD's CoP, at its 12th meeting.) In addition, the voluntary peer review identified the absence of cross-sectoral collaboration between the multiple agencies and institutions responsible for various national biodiversity targets as another critical bottleneck.

Adding to the difficulties in management is the absence of a comprehensive legislation that deals with the host of difficulties posed by invasive species across varied landscapes, unlike in many other countries. In India, we have a number of existing legislations that are invoked in the context of invasive species. An indicative list includes the Livestock Importation Act of 1898, the Destructive Insects and Pests Act of 1914, the Environment Protection Act of 1986, and the Plant Quarantine (Regulation for Import into India) Order of 2003. None of these acts or orders was devised specifically in the context of alien invasive species, however. In fact, some of these were enacted long before invasive species were ever a concern. Nonetheless, some of these lay down provisions to prevent the introduction and spread of potentially destructive organisms, but none contain provisions to comprehensively catalogue or manage existing invasive species that have spread widely across the country.

The absence of a national policy specifically on invasive species, and limited avenues for inter-sectoral collaborations on invasive species seriously hamper efforts to manage them. To be sure, increasingly there are efforts to manage invasive species (especially in protected areas), and there have also been success stories (e.g., Love et al. 2009; Babu et al. 2009). There has also been an effort to map invasive species in tiger reserves across the country (Mungi 2013). But without a coordinated national plan, these remain piecemeal efforts unlikely to have long-lasting consequences. And without the backing of a strong policy instrument, or a single nodal agency responsible for coordinating efforts pertaining to various aspects of invasive species (from prevention of introduction, to research and management) there is little likelihood of achieving our stated targets. The scale of the problem is too large to be left to multiple agencies without an overarching policy framework and coordinated plan to guide them, and a designated agency to coordinate amongst them.

Moving Towards a National Invasive Species Management Plan

Especially in the context of climate change, with current invasive species distributions predicted to change, casual alien species likely to become invasive in the future, and some pathways of invasion likely to become more important than they presently are (Hellmann et al. 2008), we need to prioritise both a comprehensive inventory of alien species and a mapping of species distributions. Additionally, we need to focus on research that generates information about underlying mechanisms of invasion and its impacts, and on outreach to create greater public awareness.

In the past couple of decades there has been a tremendous increase in research pertaining to invasive species in India (e.g., review of the literature on plant invasives; (Hiremath and Sundaram 2013). However, about a third of this literature is dominated by a single invasive species, *Lantana camara*. We still know very little about the vast majority of invasive species in India.

Having said that, while in-depth information on the ecology of individual species is important, and of interest both from a theoretical and from a management perspective, even more important – from a management perspective – would be an inventory of invasive species. Such an inventory would need to include a list of alien invasive species, information about where they come from, the mode of their introduction, a characterisation of their ecological traits, their ecological, economic and health impacts, and whether or not they are invasive elsewhere.

There have been several efforts to list invasive alien species in India, especially plants. Prominent among these are (1) a report prepared by the MoEF for the Asia Pacific Forest Invasive Species Network (APFISN) in 2005; (2) a list prepared by (Reddy et al. 2008); and (3) a list prepared by Khuroo et al. (2012). Of these, the third is perhaps the most comprehensive, and lists a total of 1599 alien plant species, categorised as invasive (225 spp.), naturalised with the likelihood of becoming invasive (134 spp.), naturalised (257 spp.), casuals that are likely to become naturalised (114 spp.), and casuals (57 spp.), the rest being species that are restricted to cultivation. Khuroo et al. (2012) base their categorisation of alien plant species on the different stages along the invasion process (Richardson et al. 2000), and as such their list is perhaps the most informative. (The other two lists provide less information about the basis on which invasive species were listed.) These existing invasive species lists are valuable efforts. Significantly, however, there is very little overlap amongst these three lists, with only 38 species in common across the three, which points to the magnitude of the challenge posed by such a task. Yet, coming up with a comprehensive list for a country the size of India, though a mammoth undertaking, is not impossible, if properly coordinated.

An example of just such an inventory comes from a pan-European programme, called 'DAISIE' (Delivering Alien Invasive Species Inventories in Europe; (Hulme et al. 2009), that has resulted in a comprehensive inventory of plant, animal, and invertebrate invasive species. The DAISIE database has since proven extremely valuable in helping to answer some very fundamental questions concerning invasive species ecology and management across Europe (e.g., (Vilà et al. 2010; Amano et al. 2016).

Also, to better refine predictions, prioritise management of species that are the most widespread, or of habitats that are most vulnerable to invasion, it is important to know where invasive species are distributed and how distributions are changing. Perhaps the best-known example of a large scale effort to map invasive species comes from South Africa. The South African Plant Invasives Atlas (SAPIA), compiled in phases over the last ~40 years, comprises a spatial database of about 50,000 records for 548 alien species across South Africa, Lesotho and Swaziland (Henderson 2007). The value of SAPIA, both to invasion biologists interested in understanding the processes underly-

BOX 1

Mapping Invasives with Smartphones in India's Western Ghats: A Plot Initiative

Milind Bunyan, Ankila Hiremath, Anita Varghese and Shiny Rehelo

Knowing where particular invasive species occur, and knowing the habitats that are most vulnerable to invasion can be very useful to managers. Baseline information on species distributions can allow us to track spread and see which species are spreading faster than others, and managers can prioritise management based on habitats that are most affected. In the context of climate change, knowledge of species' current distributions can enable us to predict potential future distributions. To better understand the distribution of invasive species, we have initiated a pilot participatory effort to map invasive species in the Nilgiris Biosphere Reserve (NBR), located in the southern half of the Western Ghats biodiversity hotspot. For this, we are making use of the Open Data Kit Collect application (ODK app), which makes it easy for researchers, practitioners, Forest Department officials, schoolchildren, college students, and citizen volunteers to identify and map invasive species using Android-based smartphones and tablets. By using the camera and GPS that smartphones come equipped with, users can provide spatially explicit, verifiable information on the location of these invasive alien plants in the landscape.

Using Citizen Science to Create an Invasives Atlas

Our collaborative mapping effort began in mid-2017 and is called Participatory Assessment of the Regional Distribution of Exotic Species in India (PARDESI; which in Hindi literally means "not from this land"). As a first step, we listed a total of 89 invasive alien plant species from the Moyar-Bhavani landscape (MBL) in the NBR, which spans an area of 4100 sq. km. and encompasses the two principal watersheds of the Moyar and Bhavani rivers. This list was then pared down to a manageable 27 species, and includes plant invasive species that represent the greatest threat to ecosystems and livelihoods across the elevation range in the landscape. An invasive species identification key was created to assist users in identifying these shortlisted invasive alien plants (Figure 1). The reverse side of this identification key has a Land Use and Land Cover (LULC) map of the landscape (Figure 2), which lead organisations can use to plan invasive species mapping efforts so that land-use types in a grid are sufficiently represented.

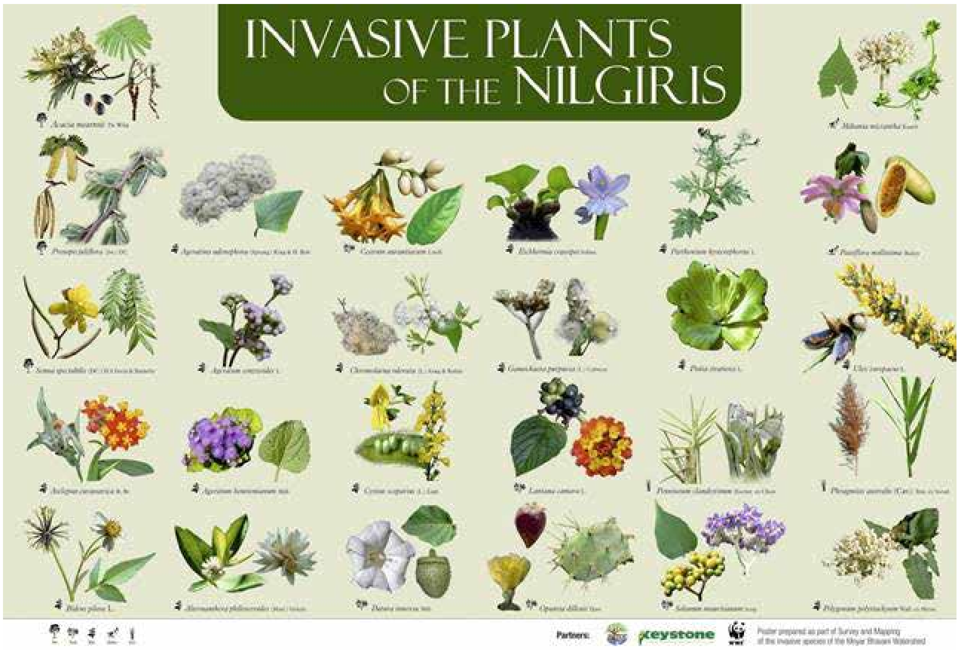

Figure. 1. Species identification key of invasive plants in the Moyar-Bhavani Landscape of the Nilgiris Biosphere Reserve (obverse face of the PARDESI poster).

Finally, in conjunction with PARDESI, which is in the pilot stage, we have conducted a series of skill-building workshops on the use of the ODK app. We have since been working with schools, higher education institutions, and forest department field staff in the region, teaching them about invasive species and their impacts, and seeking their assistance in mapping invasive species using the ODK app in the field through citizen science mapping walks.

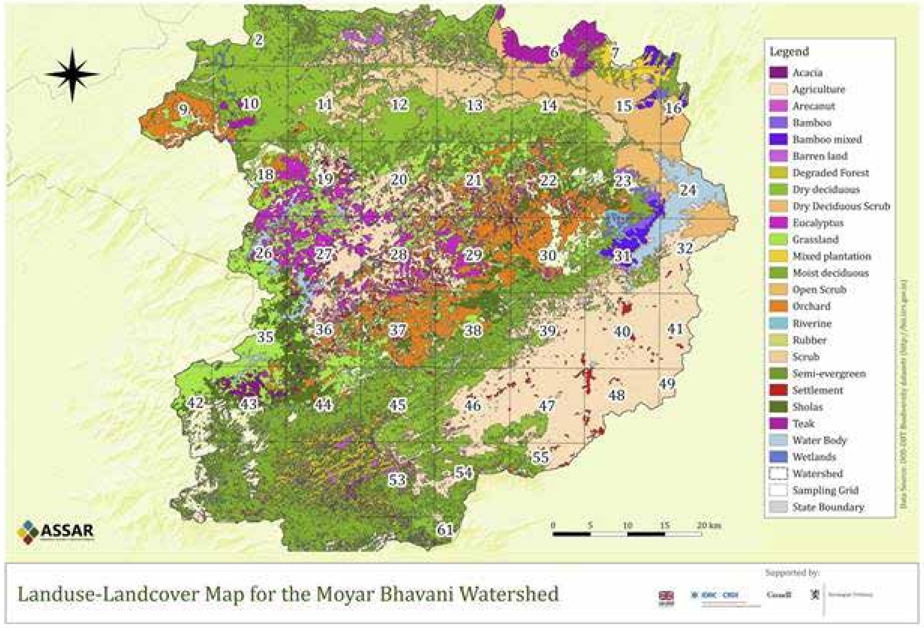

Figure 2. Land-use types in the Moyar-Bhavani Landscape of the Nilgiris Biosphere Reserve (reverse face of the PARDESI poster)

Using a citizen-science approach, PARDESI aims to create an atlas of invasive plant species, leveraging the energy and enthusiasm of communities and NGOs (and the potential this offers to survey a large area) with the expertise of research organizations. If the methodology tested in the pilot is successful, we plan to scale it up to the entire Western Ghats biodiversity hotspot and develop a long-term monitoring system in the region. This could, then, potentially serve as a model to create invasive species atlases for other large landscapes across the country.

ing invasions, and to managers interested in prioritising species and habitats to manage, has far exceeded anything that could have been envisaged (e.g., (Rouget et al. 2004; Wilson et al. 2007; Henderson and Wilson 2017). A pilot effort to try and map invasive species with the help of citizen volunteers – as was the case with SAPIA – has been initiated in the Nilgiri Biosphere Reserve in India's Western Ghats (see Box 1).

We currently lag behind in the invasive species management targets that we have set for ourselves nationally. The scale of each of the tasks ahead of us is enormous. Yet, if we proceed in a coordinated manner, involving the growing number of researchers, managers, practitioners, and citizen scientists interested in invasive species, the task would not be impossible. The National Biodiversity Authority recently established a Centre for Biodiversity Policy and Law (CEBPOL). This Centre has been given the responsibility to come up with a national invasive species management plan in consultation with all other relevant agencies. This, then, could potentially provide the coordination required to achieve our invasive species management targets.

Summary

Our chapter provides an introduction to how the interaction between invasive species spread and climate change is likely to pose significant challenges to ecosystems and society in the near future. Increasing atmospheric CO_2 and consequent global warming-induced climate change is likely to affect ecosystems properties that maintain ecological communities, including invasion by exotic species. Species invasion with changing climate is often predicted using species distribution modelling – predicting potential range of a species based on its current distribution. The starkest effect of climate change on ecosystems is likely to be shifts from current stable states to alternate states. In India, these changes and their impacts on invasive species distributions are poorly understood. However, a few case studies from local, regional, and country-wide scales indicate that invasion success (i.e., range expansion) of exotic species is likely to vary from one species to another and climate change may even make the environment unsuitable for further invasion by some species.

Theory underlying the science of invasive species spread and climate change indicates that the behaviour of species along the invasion pathway is likely to change significantly. Climate change is likely to strongly influence all stages of the invasion pathway. At the transport stage, the alteration or shift in agricultural practices due to climate change is likely to be associated with both the creation of new markets and the expansion of existing markets for cultivated species, likely increasing the rates of species transport globally. At the colonisation stage, climate change may create a set of conditions that overlap with conditions preferred by introduced species. During the establishment phase, climatic range restrictions (either shifts, expansions, or constrictions) will create conditions either favourable or unfavourable for established non-native species. Landscape spread of invasive species, however, is unlikely to be consistent across ecosystems in India, although generalist species with a broad environmental tolerance are likely to succeed more than introduced species with a restricted range of environmental tolerance.

In India, those living in poverty, who practice subsistence/marginal agriculture, or rely on forests for their primary livelihoods are likely to be strongly affected by the combined impacts of invasive species and climate change. It is highly probable that these at-risk people are pushed further into poverty due to shifts in India's biophysical economy and developmental trajectory that is becoming increasingly fossil-fuel dependent. A key conundrum that emerges as a result of such fossil-fueled development is that poverty alleviation measures that aim to raise the material living standards of the poor in India (and in other developing countries) may come at an extremely high climate cost, with this high climate cost eventually influencing how ecosystems respond to species invasions.

Although the scale of the invasive species problem is immense, there appears a reasonably clear trajectory of remedial measures, if we are to act immediately. While gaps in our knowledge on invasive species is an issue, an important hurdle to overcome is the absence of a comprehensive regulatory framework that addresses each stage of the invasion pathway. Such a regulation would specify funding mechanisms, as well as the coordinating agency, the lack of clarity relating to both these aspects being key reasons for the continued lapses in our management of the problem. Invasive species provide a unique opportunity for researchers and policymakers to join forces. In fact, if we are to ever have a shot at effectively addressing the issue, it is imperative that they do.

As we have shown, a climate-altered future is likely to exacerbate the negative impact of invasive species in the ecological and social sense, but is likely to pose questions of a philosophical nature as well. The reach of the Anthropocene, defined as a human-caused geological era mediated by climate change and species introductions, does not

Lantana *craft at Male Mahadeshwara Hills (Photo: Narayanan B)* exclude any ecosystem in the world. Humans may have to reimagine their role in such a system as gardeners living in a "half-wild, rambunctious garden tended by us" (Marris 2011, Pp. 3). A pragmatic approach to managing invasive species may be required in this rambunctious garden by weighing the costs and benefits of invasive species, especially when the invasive species in focus has perceived positive effects. The invasive *Prosopis juliflora*, which has invaded dry forests and grassland savannahs in parts of west and south India is an interesting case in point. Although this species has negative effects in systems it has invaded, local communities have 'socialised' this species, and use it to generate wood-charcoal. Similarly, *Lantana camara*, which has invaded large swathes of the country, is being used by artisans for furniture and handicrafts, and by farmers as mulch. At one level therefore, management (rather than eradication) of some that stems from an acceptance that some invasive species are here to stay, is likely more pragmatic in the long run.

Given the sheer number of introduced species in India, and very little data on the invasive potential of these species, it is clear that prioritisation of invasive species management has to be pragmatic and multi-pronged. While we need to focus on early detection, and prevent the introduction of known invasive species, we also need to focus management on threatened ecosystems of high biological value, such as the Western Ghats and Eastern Himalaya biodiversity hotspots. At the same time, we may need to accept that some ecosystems have been irreversibly transformed into novel social-ecological systems, where invasive species have become integrated into local livelihoods and cultures. An agenda for further research on the effects of invasive species and climate change will be strongly enabled through the creation, compilation, and regular updation of nation-level databases. Due to the complexity posed by the interactive effects between invasive species spread and climate change, the high level of coordination that is required between government agencies such as MoEFCC, scientists, and civil society – both urban and rural – is likely to emerge as a systemic constraint and challenge.

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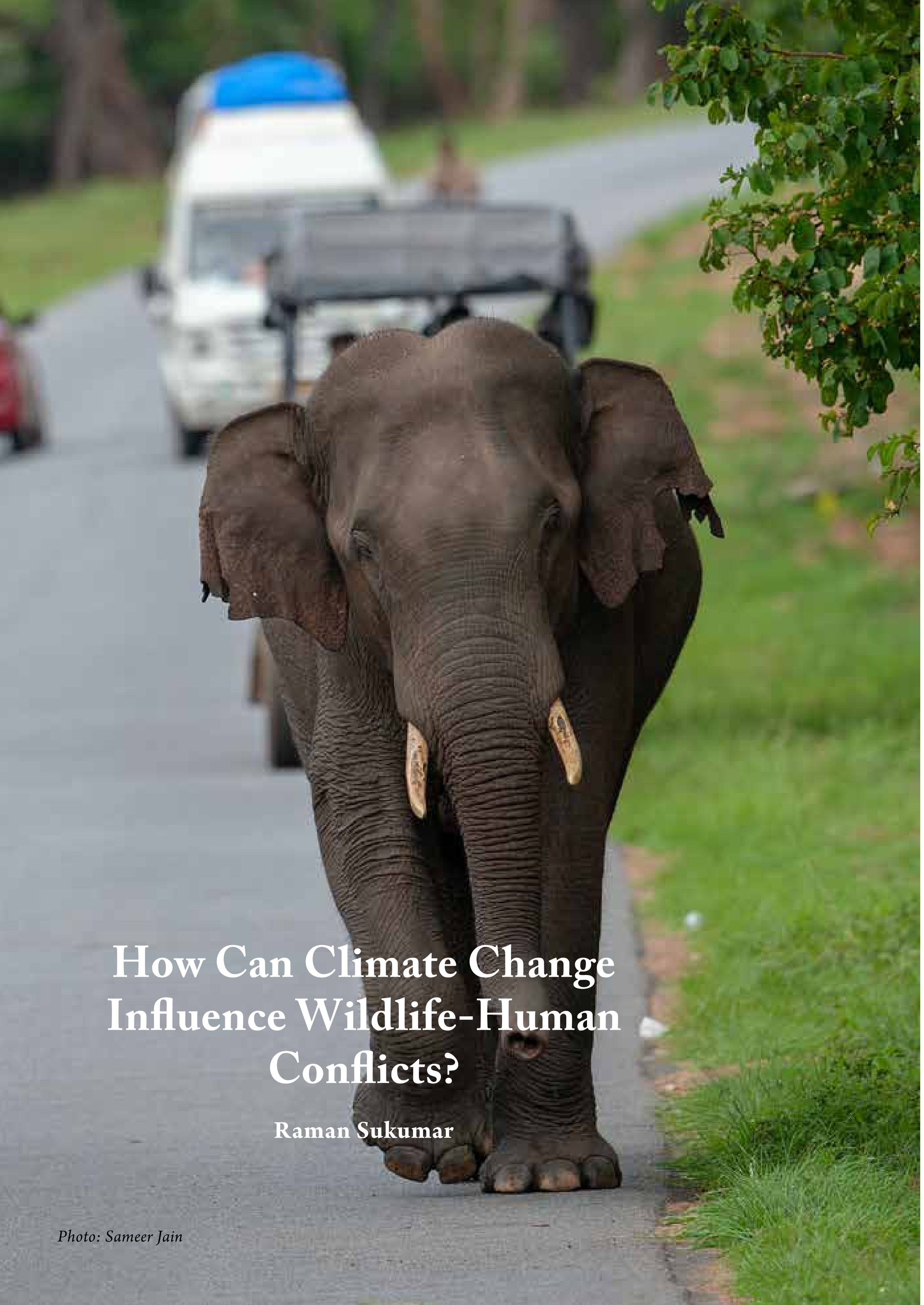

How Can Climate Change Influence Wildlife-Human Conflicts?

Raman Sukumar

Photo: Sameer Jain

INTRODUCTION

Climate change is expected to make significant impacts on plant and animal communities with consequences for their population dynamics, distribution and interface with human land-use in the coming decades (Settele et al. 2015). While there have been several studies and modelling exercises on the probability of survival (or extinction) of several plant and animal species (Brook et al. 2000), including in a climate change context (Keith et al. 2008), the aspect of negative consequences of the interactions between animals and people expected under a changing climate has received little attention (Gupta et al. 2017). Conflicts between wildlife and people are now recognised as a major dimension to be addressed in conservation planning (Sukumar 1994a; Madden 2004; Woodroffe et al. 2009). Such conflicts, both direct (e.g. human deaths due to wildlife) and indirect (e.g. loss of agricultural crops, property and livestock to wildlife depredation) have always happened through history, but in recent times have escalated regionally in parts of the world and particularly in India. The broad ecological and social dimensions of wildlife-human conflicts are being addressed in a number of studies (Sillero-Zubiri et al. 2007; Dickman 2010; Sukumar 2016), but the link between climate change and such conflicts is still understudied in the country and elsewhere.

A global review of 113 published studies listing 524 recommendations relating to biodiversity management in the face of climate change (Heller and Zavaleta 2009) lists only one paper (Wilby and Perry 2006) which mentions the need to manage wildlife-human conflicts, and that too in an urban context. Another review of climate change adaptation for wildlife management and biodiversity conservation (Mawdsley et al. 2009) does not even mention wildlife-human conflicts (with the exception of increased spread of zoonotic diseases – an indirect impact) among a core set of 16 adaptation strategies commonly considered in the literature.

Wildlife-human conflicts are the result of a complex interplay of ecological and behavioural factors which have been categorised into the so-called ‘proximate causes’ (e.g. land-use change, increase in wildlife populations) and ‘ultimate causes’ (e.g. optimal foraging, animal behavioural ecology) in the language of evolutionary biology (Sukumar 2016). Climate-related factors can be considered as one proximate cause of wildlife-human conflicts (Sukumar 2016; Gupta et al. 2017) both in the short and long term. We can consider the role of climate in driving conflicts from the point of view of short-term climate variability which triggers changes in animal movement or dispersal patterns, as well as long-term climatic trends that influence plant and animal distribution. A survey of the literature shows that a few studies have recognised the role of climate variability in determining the levels of conflict, but hardly any studies have explored the role of systemic climate change – and so this aspect has to largely remain speculative.

CLIMATE VARIABILITY AND CONFLICTS

Most regions of the world experience strong seasonality in climate and even the equatorial region, considered the least seasonal of the latitudinal belts, is subject to limited intra-annual variation in rainfall. Animal movements are strongly influenced by seasonality (Birkett et al. 2012) and the links between such seasonal movements and conflicts in the form of crop raiding, livestock predation, or even human deaths have been established in some species. For instance, many studies have shown that crop raiding by herbivorous animals and livestock predation by carnivores may be distinctly seasonal. Thus, elephant raiding of cereal crops typically peaks towards the end of the rains and the beginning of the dry season when the plants flower or set grain and are ready for harvest (Sukumar 1989, 2003; Osborn 2004; Chiyo and Cochrane 2005), while African lion (*Panthera leo melanochaita*) and leopard (*Panthera pardus*) attacks on livestock held within 'kraals' increases during the dry season (Butler 2000), though large carnivore attacks on livestock in some areas may intensify during the wet season when natural prey are more difficult to locate because of poor visibility under conditions of luxuriant vegetation (Patterson et al. 2004; Kolowski and Holekamp 2006).

While a certain degree of variation in seasonal weather patterns is inherent to the climatic regime of any region, an increase in the variability of rainfall or temperature can impact the availability of water, vegetation and food resources for animals. Extreme or prolonged droughts are the most obvious case of climatic variability with highly significant consequences for plant and animal populations, as well as levels of wildlife-human conflicts. At the same time, even the "normal variation" in weather on inter-annual time scales can influence short-term changes in animal movement patterns and thus, the locations and extent of conflicts.

The links between El Niño Southern Oscillation (ENSO) and severe disruptions to global weather patterns is well known. The warm phase of ENSO, termed as El Niño typically causes droughts in the Southern Hemisphere and southern Asia (Kousky et al. 1984) as well as floods in other regions such as southern South America (Schöngart and Junk 2007). There are a few documented cases of wildlife-human conflicts escalating during periods of severe drought, and it is worth giving an example each for a large herbivore (the Asian elephant, *Elephas maximus*) and a large carnivore (the Asiatic lion, *Panthera leo persica*) from India.

*Elephant (*Elephas maximus*) being driven away using vehicles (Photo: Sreedhar Vijayakrishnan)*

Elephant Dispersals and Conflicts in India

The El Niño event of 1982 has been described as perhaps the strongest such climatic phenomenon of the 20th century (Kousky et al. 1984). The Indian monsoon weakened considerably over the peninsula; this resulted in a rainfall deficit of over 40% from the normal across a large part of the Asian elephant's range in the Eastern Ghats of southern India (Sukumar 1985) causing a sharp decline in vegetation productivity. The few hundred elephants in Hosur Forest Division (Tamil Nadu), the easternmost part of the elephant's range in the south, is part of the largest single population of Asian elephants in the continent. The deciduous forests of this region were already under pressure from the resource extractive activities of a number of human settlements within this forest division (Kumar 1994). Beginning in 1984, several herds of elephants dispersed from the forests of Hosur and adjoining areas of Bannerghatta (Karnataka) northwards through a series of patchy forests into the Chittoor Forest Division of Andhra Pradesh, a region where wild elephants were unknown for a few hundred years.

The first dispersal seems to have been a herd of seven elephants from Hosur in March 1984, while another herd of 22 elephants from Bannerghatta was reported to have moved into Chittoor in 1986 (Sivaganesan and Bhushan 1986; Prasad and Reddy 2002). From reports of elephant deaths and other evidence, it is clear that many more elephants had moved to Andhra Pradesh from Tamil Nadu and Karnataka during the 1980s (Manakadan et al. 2010). The ensuing conflict with agriculture and people has been described in a number of anecdotal accounts and reports (Sivaganesan and Bhushan 1986; Rao 1995), but the link with the ENSO event seems to have been explicitly recognised only later (Sukumar 1995). This dispersal has involved well over a hundred elephants (Manakadan et al. 2010).

There was a sharp escalation in conflicts with people and agriculture with at least 30 people killed in the first ten years following the dispersal (Rao 1995). Many of the human deaths were attributed to a single, particularly aggressive female elephant. At the same time, the people in Andhra Pradesh were unfamiliar with wild elephants and the dangers of approaching them closely - from 1985 to 1999, 45 people were killed and 13 were injured in the Koundinya Wildlife Sanctuary region (Manakadan et al. 2009). These casualties were the result of people being curious to see elephants, protecting crops from being raided and chance encounters on forest trails (Manakadan et al. 2009). Twenty four elephants were killed between 1987 and 2003, and over half these deaths were attributed to electrocution by power lines villagers had set up to prevent crop damage by wild boars (Manakadan et al. 2009).

The Indian monsoon was again substantially in deficit during 1986-1987 following another strong El Niño phase. One more significant dispersal of elephants occurred, this time from Jharkhand (in erstwhile Bihar) to southern West Bengal. Beginning around 1987, about 40-50 elephants from Dalma Wildlife Sanctuary began to move deeper into West Bengal (Sukumar 1994b; Singh et al. 2002). Although elephants had historically been visiting the border areas of West Bengal, the incursions during the late 1980s became more persistent, initially with the Jhargram Forest Division and later into several forest divisions in three districts (Subhamay Chanda: undated report on man-elephant conflict in southwest Bengal). Conflict quickly escalated with damage to paddy crop and, more importantly, human deaths due to elephants (Figure 1).

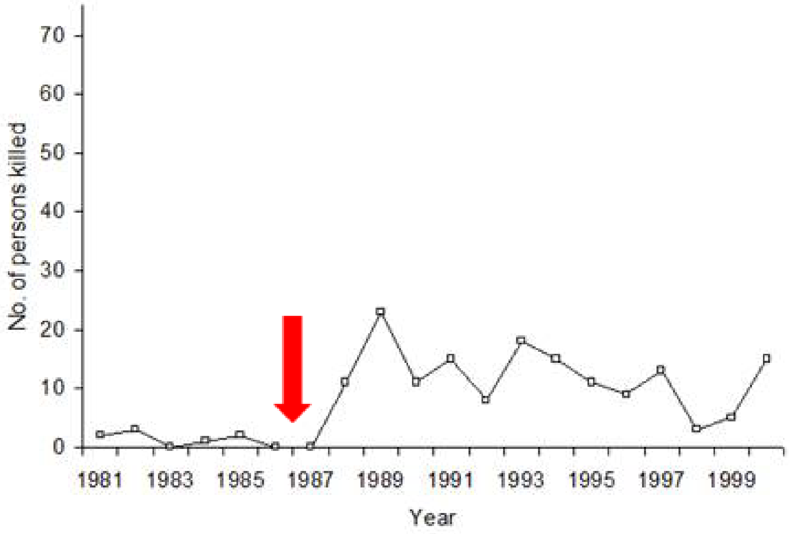

Figure 1. Number of people killed by elephants in south Bengal between 1980 and 1999. Arrow indicates El Niño event in 1986. Based on Sukumar (2003)

Today, over 150 elephants are present across a mosaic of relatively small patches of Reserved Forests, village forests, and large expanses of agricultural production areas mainly in the districts of West Medinipur, Purulia and Bankura. The overall range of the elephant covers an area of several thousand km^2, a large part of it being agricultural land. The conflict between elephants and people is intense with increase in the number of elephants entering West Bengal, changes in the movement patterns of the herds, newer incursions into districts such as Burdwan district, and more elephants becoming resident in southwestern Bengal rather than returning to Jharkhand (Kulandaivel 2012, unpublished report, West Bengal Forest Department). In 2015, the number of people killed by elephants reached a peak of 71 individuals.

A combination of environmental factors was responsible for the dispersal and persistence of elephants in southern West Bengal. First, the natural habitat in Jharkhand had already been subject to considerable degradation from mining, conversion of sal (*Shorea robusta*) forest to teak (*Tectona grandis*) plantations, and deforestation in the early 1980s resulting from the agitation launched by adivasis (under the 'Jungle Bachao Andolan' movement) against such forest conversion meant that the elephants were already under pressure. Second, the success of the social forestry programme in southern Bengal resulted in regenerating patches of sal, but also planted forests of exotic eucalypts and *Acacia auriculiformis* which, ironically, served as daytime refuges for the dispersing elephants, thus enabling them to raid the nearby paddy fields at night. However, the drought of 1986-1987 was probably the 'climatic trigger' for the elephants to move deep into southern West Bengal in search of adequate forage.

Lion-Human Conflicts in the Gir Forest

One of the best-documented cases of increased wildlife-human conflicts as a possible response to a severe drought comes from a study of lion-human conflicts during 1978-1991 in the Gir forests of western India (Saberwal et al. 1994). The Asiatic lion population, then numbering an estimated 250-300 individuals, was confined to this single

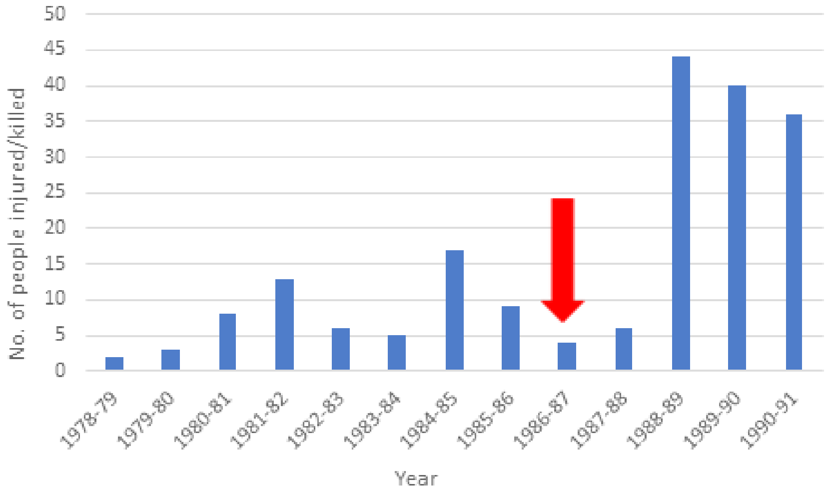

Figure 2. Number of people injured or killed by lions in and around Gir Forest, Gujarat, 1978-1991. Red arrow indicates the occurrence of severe drought associated with El Niño that began in March 1986 and ended in June 1988. Based on data presented in Saberwal et al. (1994).

protected area of about 1400 km^2, also home to a buffalo-pastoralist people, the Maldharis. Although lions prey upon buffaloes fairly regularly (livestock constitute about a third of the lion's diet), attacks on people were generally low at 7.3 attacks and less than one human death on average per year until 1987. In response to the 1986 ENSO phase, this region experienced a serious drought that began by mid-March 1986 and persisted until the onset of the monsoon in June 1988. The number of human attacks sharply increased to 40, with 6.7 deaths per year for three years (1988-1991) following the drought (Figure 2). Even more striking was that the lions, which had never eaten humans in several years prior to the drought, now consumed human flesh in some of these incidents. A similar spate of lion attacks on people had been recorded here during 1901-1904 following the severe drought of 1899-1900 (Wynter-Blyth and Dharmakumarsinhji 1950).

The authors speculate upon possible drought-related causes for the enhanced levels of conflict. Poorer villages close to the park boundary seem to have suffered higher losses of livestock during the drought, thus forcing the lions to move further away from the park in search of prey. Lion attacks on people actually increased during the monsoon period when both lions and people were active during the day, while the denser vegetation could have increased the chances

Adult male Asiatic lion (Panthera leo) *in Gir Forest, Gujarat (Photo: Sumeet Moghe; Wikimedia Commons)* of accidental close encounters between them. Clearly, drought triggers a complex interplay of factors which finally manifest in increased human deaths in large carnivore attacks.

SYSTEMIC CLIMATE CHANGE AND CONFLICTS

The ongoing climate change, largely attributed to anthropogenic greenhouse gas emissions, has already raised the average global (surface and ocean) temperature by 0.85 to 1.06°C during 1880-2012 with accompanying regional changes in other climatic factors such as precipitation (IPCC 2014). There is also clear evidence of climate change-induced impacts on plant and animal communities worldwide (Parmesan and Yohe 2003); among the impacts are changes in species distribution, phenology or life history events, birth and death rates, competitive interactions among species, and increased spread of invasive or non-native species. These have the potential to have a direct bearing on wildlife conflicts with people. While the global warming trends contribute to species migration along altitudinal (typically lower to higher elevation) or latitudinal (equator towards the poles) gradients, changes in regional precipitation patterns can cause confounding responses by species trying to adapt to the changing environment. In southern Africa, for instance, a shift in the coupled ocean-atmospheric system since the late 1970s has already resulted in decreased average rainfall with increased interannual variation and increase in the frequency of El Niño events across the Okavango-Kwando-Zambezi catchment, a region rich in wildlife (Gaughan and Waylen 2012); this has the potential to decrease flow in the three rivers, change animal movements and increase wildlife-human conflicts, especially during the dry season.

In the Indian subcontinent, there seems to be only a single study that has explicitly considered the role of systemic climate change in increasing wildlife-human conflict; this comes from the Trans-Himalaya region of Nepal (Aryal et al. 2014). The average annual temperature of the upper Mustang region (elevation above 3000 m) had been increasing at the rate of 0.13°C per year or by 3.0°C between 1987 and 2009, a considerable warming trend which is reflected in the changing vegetation composition, water availability and loss of land suitable for cultivation. During the period 1979-2009, satellite data showed that grasslands and forests in the Mustang district reduced by 11% and 42%, respectively. Correspondingly, the treeline in the district shifted to higher elevation.

This change in vegetation patterns has cascaded down to the movement patterns of wildlife species and their interface with people. With decrease in grass and many shrubby plants, blue sheep (*Pseduois nayaur*) have been moving to lower elevations to meet their foraging requirement while at the same time, raiding cultivated crops in villages located below. Snow leopards (*Panthera uncia*) have increasingly followed their prey, blue sheep, to the lower elevations and predated on livestock. This is a classic case of how ongoing systemic climate change has caused impacts at various levels, from changes in vegetation through altered animal movement patterns to consequences for people's livelihoods.

As people try to adapt to a changing climate, especially to obtain food, there could be significant changes in land use for cultivating crops (Gibbs et al. 2010). This could result in agriculture spreading into areas which are presently under some form of natural vegetation cover with wildlife populations. We can only speculate that such conversion of forests into agriculture as climate-adaptation would result in increased wildlife-human conflicts as seen from similar conversions in non-climate contexts.

Bengal tiger (Panthera tigris) *in the Sundarbans (Photo: Soumyajit Nandy; Wikimedia Commons)*

Climate change may also exacerbate wildlife-human conflicts in other indirect ways. One of the consequences of increasing temperatures is sea level rise through thermal expansion of water, melting ice sheets in the Antarctic, Arctic and Greenland, and melting glaciers in the high mountains (Nerem et al. 2006). While there are varying estimates of the rate of sea level rise globally or regionally, among the most vulnerable places are estuarine regions such as the Sundarbans of Bangladesh and India, home to the most extensive mangroves in the world and a significant population of the tiger (*Panthera tigris*). A modelling exercise of sea level rise in the Bangladesh Sundarbans, taking a figure of 4 mm year^{-1} (from the baseline year 2000) as a conservative estimate, found that by the year 2070 the sea level rise of 280 mm will submerge 96% of the tiger's present range rendering the habitat unviable for the survival of the species (Loucks et al. 2009). With sea level rise we can also expect tigers to disperse further inland with increased levels of conflicts with people and livestock.

MITIGATING CLIMATE CHANGE RELATED WILDLIFE-HUMAN CONFLICTS

The effective mitigation of wildlife-human conflicts, even in the absence of climate-related causes, is a major challenge for managers and conservationists (Messmer 2000; Madden 2004). Short of lethal options, there has been limited success in containing the direct impacts of many species of wildlife on agriculture, livestock and people. Climate change is an additional dimension to an already complex conservation problem. There are no easy solutions on how to deal with climate-related conflicts. While it is beyond the scope of this article to provide a detailed account of wildlife-human conflict


Photo: Manjunath N B

mitigation options, two broad approaches to minimize the risk of climate-related conflicts can be mentioned here.

1. Landscape-scale planning for wildlife conservation: Under a changing climate, both plant and animal populations will have to adapt through gradual migration as well as dispersal to more suitable habitats for their survival. It is difficult to anticipate the precise nature of dispersals, but the adaptation process can be facilitated at the landscape-scale through regulations on land-use, wildlife corridors, and a system of incentives to people for maintaining biodiversity-friendly land-use (Sukumar 2016; Sukumar et al. 2016). This would be the best insurance against overall species extinction and escalation of wildlife-human conflicts related to climate change.

2. Control of large animal dispersals into human-production habitats: There is a real danger of climate change induced dispersals of large mammals into predominantly agricultural areas and densely settled places causing sharp escalation in conflicts with people. Concurrent with landscape-scale planning, it is important to put in place clear policies on how to contain wildlife (both as individuals or as groups and subpopulations) in such human-production habitats while also maintaining a viable population of the species for conservation.

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APPENDIX A

List of studies addressing climate change impacts on ecosystem services in India published between 2000 and 2018, along with type of study (empirical, modeling, review, or a combination of these approaches), region of focus, ecosystem service response as described by the authors of the respective studies, and ecosystem service according to the classification by Costanza et al. (Costanza et al. 1997) (also see Table 2).

No	Reference	Study type	Focal region	Response studied	Service category
1	(Aggarwal and Mall 2002)	Modeling	India	Rice yield	Food production
2	(Saseendran et al. 2000)	Modeling	Kerala	Rice yield	Food production
3	(Guhathakurta et al. 2011)	Empirical + review	India	Flood risk	Disturbance regulation
4	(Auffhammer et al. 2012)	Empirical	India	Rice yield	Food production
5	(Mall et al. 2004)	Modeling	India	Soya production	Food production
6	(Attri and Rathore 2003)	Modeling	India	Wheat production	Food production
7	(Meenu et al. 2013)	Modeling	River Tungabhadra	Stream flow and evapotranspiration	Water supply and regulation
8	(Kumar et al. 2011)	Modeling	Western Ghats	Crop production	Food production
9	(Byjesh et al. 2010)	Modeling	India	Maize production	Food production
10	(Falloon et al. 2007)	Modeling	India	Vegetation and soil carbon	Gas regulation
11	(Srivastava et al. 2010)	Modeling	India	Sorghum production	Food production
12	(Gosain et al. 2011)	Modeling	India	Water resources	Water supply and regulation
13	(Vass et al. 2009)	Empirical	River Ganga	Fisheries	Food production
14	(Narsimlu et al. 2013)	Modeling	Upper Sind River	Water resources	Water supply and regulation
15	(Soora et al. 2013)	Modeling	India	Rice yield	Food production
16	(Rehana and Mujumdar 2011)	Modeling	River Tungabhadra	Water quality	Water supply and regulation
17	(Mathauda et al. 2000)	Modeling	Punjab	Rice yield	Food production
18	(Birthal et al. 2014)	Empirical + modeling	India	Crop yields	Food production
19	(Islam et al. 2012)	Modeling	River Brahmani	Stream flow	Water supply and regulation
20	(Kumar et al. 2014)	Modeling	India	Wheat production	Food production
21	(Kumar and Aggarwal 2013)	Modeling	India	Coconut production	Food production
22	(Manish et al. 2016)	Modeling	Sikkim	Plant community composition	Refugia
23	(Srivastava et al. 2015)	Remote sensing	Gulf of Kutch	Mangrove distribution	Refugia
24	(Gopalakrishnan et al. 2011)	Modeling	India	Teak production	Raw materials
25	(Hebbar et al. 2013)	Modeling	India	Cotton production	Raw materials
26	(Dubey et al. 2014)	Modeling	Uttarakhand	Wheat production	Food production
27	(Palanisami et al. 2011)	Modeling	River Godavari Basin	Crop production	Food production
28	(Upgupta et al. 2015)	Modeling	Western Himalaya	Forest distribution	Refugia
29	(Palanisami et al. 2014)	Review	India	Crop production	Food production
30	(Singh and Kumar 2015)	Modeling	India	Water availability	Water supply and regulation
31	(Jayaraman and Murari 2014)	Review	India	Crop production	Food production
32	(Das et al. 2013)	Empirical	River Ganga	Fisheries	Food production
33	(Kumar et al. 2015)	Modeling	Gangetic Plain	Potato production	Food production
34	(Vashisht et al. 2013)	Modeling	Punjab	Wheat production	Food production
35	(Sarma et al. 2015)	Modeling	India	Species invasion	Biological control
36	(Abeysingha et al. 2016)	Modeling	India	Rice and wheat production	Food production
37	(Pechlivanidis et al. 2015)	Modeling	Luni Rajasthan	Water resources	Water supply and regulation
38	(Kumar et al. 2007)	Empirical	Himachal Pradesh	Glacier mass	Water supply and regulation
39	(Gupta et al. 2011)	Modeling	Indian river basins	Runoff	Water supply and regulation

No	Reference	Study type	Focal region	Response studied	Service category
40	(Ravindranath et al. 2006)	Modeling	India	Forest productivity	Gas regulation
41	(Pritchard 2016)	Review	India	Food and nutrition	Food production
42	(Dutta 2014)	Modeling	Northeast India	Tea production	Food production
43	(Gupta et al. 2010)	Modeling	Indian river basins	Runoff	Water supply and regulation
44	(Pandey et al. 2009)	Modeling	Gujarat	Crop yields	Food production
45	(Yadav et al. 2015)	Modeling	Varanasi	Cereal production	Food production
46	(Mondal and Mujumdar 2015)	Modeling	India	Stream flow	Water supply and regulation
47	(Khare et al. 2017)	Modeling	Mandakini River	Soil erosion	Erosion control and sediment retention
48	(Saxena and Kumar 2014)	Modeling	India	Rice production	Food production
49	(Deb and Babel 2015)	Modeling	East Sikkim	Maize production	Food production
50	(Moorthy et al. 2012)	Empirical	India	Crop yields	Food production
51	(Mishra et al. 2016)	Modeling	Odisha	Crop yields	Food production
52	(Mondal et al. 2016)	Modeling	Central India	Rainfall erosivity	Erosion control and sediment retention
53	(Mahmood and Jia 2016)	Modeling	Jhelum River	Water resources	Water supply and regulation
54	(Madhusoodhanan et al. 2016)	Review	India	Water resources	Water supply and regulation
55	(Kizhakudan et al. 2014)	Empirical	Tamil Nadu	Fisheries	Food production
56	(Singh et al. 2017)	Modeling	India	Rice production	Food production
57	(Dobhal and Pratap 2015)	Empirical	Uttarakhand	Glacier mass	Water supply and regulation
58	(Chatterjee et al. 2014)	Modeling	Damodar River	Water resources	Water supply and regulation
59	(Singh et al. 2016)	Review	India	Apple production	Food production
60	(Priya et al. 2014)	Empirical + modeling	Varanasi	Evapotranspiration	Water supply and regulation
61	(Kumar et al. 2017)	Modeling	Upper Kharun River	Water resources	Water supply and regulation
62	(Mohanty et al. 2015)	Modeling	Central India	Soya production	Food production
63	(Nune et al. 2013)	Modeling	Musi River basin	Stream flow	Water supply and regulation
64	(Sen et al. 2016)	Modeling	Western Ghats	Pepper distribution	Food production
65	(Mudbhatkal et al. 2017)	Modeling	South India	Stream flow	Water supply and regulation
66	(Kambale et al. 2017)	Modeling	North India	Groundwater recharge	Water supply and regulation
67	(Basu 2010)	Empirical + review	West Bengal	NTFP	Genetic resources
68	(Padmavathi and Virmani 2013)	Empirical	India	Safflower production	Food production
69	(Kathmale et al. 2013)	Empirical	Maharashtra	Soya production	Food production
70	(Khan et al. 2016)	Modeling	Tamil Nadu	Mangrove distribution	Refugia
71	(Singh and Kumar 2014)	Empirical	Himachal Pradesh	Glacial lake outburst flood	Disturbance regulation
72	(Sarkar and Borah 2018)	Review	India	Floodplain wetland fisheries	Food production
73	(Patil 2016)	Modeling	Rangandi River	Streamflow	Water supply and regulation
74	(Reddy et al. 2016)	Modeling	Krishna River Basin	Maize water balance	Food production
75	(Raj et al. 2018)	Empirical	Malvan Marine Sanctuary	Coral bleaching	Refugia
76	(Jana et al. 2015)	Modeling	Subarnarekha River Basin	Stream flow	Water supply and regulation
77	(Yadav et al. 2016)	Modeling	Varanasi	Crop production	Food production
78	(Jain and Mishra 2016)	Empirical	Hoshangabad	Water quality and diseases	Waste treatment
79	(Zacharia et al. 2016)	Review	India	Coastal fisheries and aquaculture	Food production
80	(Vandana et al. 2018)	Modeling	Brahmani River basin	Stream flow	Water supply and regulation
81	(Jana et al. 2015)	Modeling	Eastern India	Groundwater recharge	Water supply and regulation
82	(Geethalakshmi et al. 2017)	Empirical	Tamil Nadu	Rice production	Food production
83	(Singh et al. 2018)	Modeling	Chittorgarh	Water resources	Water supply and regulation

No	Reference	Study type	Focal region	Response studied	Service category
84	(Saraf and Regulwar 2018)	Modeling	Godavari Basin	Runoff	Water supply and regulation
85	(Chakravarthy et al. 2017)	Modeling	India	Maize production	Food production
86	(Kumar et al. 2013)	Review	India	Water resources	Water supply and regulation
87	(Patil et al. 2015)	Modeling	India	Fruit production	Food production
88	(Das and Nanduri 2018)	Modeling	Wainganga Basin	Stream flow	Water supply and regulation
89	(Haris et al. 2014)	Modeling	Pusa	Cereal production	Food production
90	(Bhagawati et al. 2017)	Review	Arunachal Pradesh	Crop production	Food production
91	(Paul et al. 2017)	Empirical	Cachar district	Crop production	Food production
92	(Maikhuri et al. 2017)	Review	Central Himalaya	Medicinal plant availability	Genetic resources
93	(Sandeep et al. 2018)	Modeling	India	Sorghum production	Food production
94	(Shekhar et al. 2018)	Review	Multi	Toxins in maize	Food production
95	(Jin et al. 2018)	Empirical and modeling	Mahanadi	Water flow and quality	Water supply and regulation
96	(Whitehead et al. 2018)	Modeling	Multiple rivers	Water quality and quantity	Water supply and regulation
97	(Mohanty et al. 2017)	Review	India	Fisheries	Food production
98	(Mrinmoy et al. 2015)	Modeling	India	Rice yield	Food production
99	(Ghosh et al. 2018)	Empirical	Sunderbans	Meiobenthic communities	Refugia
100	(Jain and Singh 2018)	Review	Ganga	Water quality and quantity	Water supply and regulation
101	(Hussain et al. 2018)	Empirical	Hoogly	Groundwater recharge	Water supply and regulation
102	(Sony et al. 2018)	Modeling	Western Ghats	Nilgiri Tahr distribution	Refugia

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APPENDIX B

A summary of phenology studies from India since 1982. Location, phenophases and key results are highlighted here.

No.	Study site (lat, long)	Forest type, elevation & annual rainfall	Years	Method, Species nos; individuals	Phenophases	Leaf flush/fall	Flowering peak	Fruiting peak	Climate variables	Reference
1.	Lailad, Khasi Hills, Meghalaya, north-east India; 25°45′-26°N, 91°45′-92°N1	Subtropical humid forest; 296 m; 220 cm	1979-1980	122 spp.	Fortnightly/ monthly; leaf flush, leaf fall, flower buds, flowers, unripe/ ripe fruits	Leaf fall: Jan-Mar Leaf flush: Mar- June	Flower bud: Feb-Mar Flowers: Apr	Ripe fruit peak: July-Aug; Overall period: May-Sept	No	Shukla and Ramakrishnan 1982
2.	Bandipur TR, south India 11°39N, 76°37′E	Tropical dry deciduous; 79-200 cm	Apr 1975-Dec 1976; Feb 1978-Sep 1979	1-ha plot; *29 spp.; 381trees GBH > 5 cm	Fortnightly; Leaf flush, mature leaf, old leaf/leaf fall, flower bud, mature flower, flower fall, unripe fruit, mature fruit, fruit fall	Leaf flush: Apr-June Leaf fall: Oct-Dec	Flower bud/flower: Feb- Aug	Unripe/ripe fruit: May-July Fruit fall: Dec-Feb	No	Prasad and Hegde 1986
3.	Uttara Kannada, south India 13°55 - 15°31′N; 74°9′ to 75°10′E	Tropical moist forest; 50-600 m; 120 to 500 cm	Nov 1983-Dec 1985	Eight one-ha plots 103 spp.; 4779 trees GBH > 10 cm	Fortnighly; Leaf flush, mature leaf, old leaf/leaf fall, flower bud, mature flower, flower fall, unripe fruit, mature fruit, fruit fall	Feb-Mar	Dec, Mar	May-June	No	Bhat 1992
4.	Mudumalai TR, Tamil Nadu, south India 11°30′ - 11°39′N, 77°27′ - 77°43′E	Tropical dry deciduous and dry thorn forest 1000 m; 110 cm, 60 cm	Apr 1988 - Aug 1990	Site 1: 38 spp.; 286 trees Site 2: 27 spp.; 167 trees DBH > 10 cm	Young leaf, expanding leaf, mature leaf and old leaf	January-May/ June	NA	NA	Yes; rainfall data; time lag correlations of rainfall with leaf flush – 2 months prior to rains	Murali and Sukumar 1993
5.	Mudumalai TR, Tamil Nadu, south India 11°30′ - 11°39′N, 77°27′ - 77°43′E	Tropical dry deciduous and dry thorn forest; 1000 m; 110 cm, 60 cm	Apr 1988 - Aug 1990	Site 1: 38 spp.; 286 trees Site 2: 27 spp.; 167 trees DBH > 10 cm	Flower bud, open flower, young fruit, developing fruit, mature fruit	NA	Site 1: Jan-Mar (late dry season), Site 2: Apr-July (Wet season)	Site 1: Aug-Dec Site 2: Jan-Feb	Yes	Murali and Sukumar 1994
6.	Thithimathi Reserved Forest 12°13′N, 76°00′E; Makut Reserved Forest 12°05′N, 75°44′E	Seasonal deciduous, 850-1350 m 1486mm, and tropical evergreen, 60-1900m, 5259mm	104 weeks (1990-1992)	Opportunistic, Site I: 2 spp. (Ficus exasperata, 53 trees and F. hispida, 28 trees) Site 2:2 spp. (Ficus exasperata, 28 trees and F. hispida, 33 trees)	Weekly, Syconium development	NA	NA	F. exasperata, both sites - Receptive phase: Male trees- Jan-May, Female trees – Mar-June; F. hispida Male- Jan-May, Female- Mar-June but also year round.	NA	Patel 1996
7.	Kakachi, KMTR, Western Ghats, south India 8°33′N, 77°23′E	Wet evergreen forest; 1300 m, 300 cm	Jan 1991-May 1993	Cullenia exarillata for flowering; few other spp. for fruiting	Flowers, fruits	NA	Feb-May (dry season)	May-Sept	No	Ganesh and Davidar 1997
8.	Thithimathi & Makut Reserve Forest, Coorg, Karnataka, south India; 12°13' N, 76°00′ E; 12°05′ N, 75°44′ E	Deciduous forest (dry site); 167 cm; Evergreen forest (wet site); 635 cm	Jan 1991-May 1992	7 fig spp.; 13 non-fig tree spp., 130 trees (> 10 cm DBH)	Weekly; flowers, fruit, leaf flush Scoring: 0-4 (1 = 25%, 2 = 50%, 3 = 75%, 4 = 100%)	Dry site: Leaf flushing middle of dry season; Wet site: both dry periods; Fig leaf flush at same time as non-figs in dry site but not in wet site	Dry site: Jan-Apr and post-monsoon; Wet site: Most of year except monsoon, peak in Jan	Dry site: Dry early season, post-monsoon; Wet site: Fruiting followed flowering with some overlap Figs before flower/ fruit of non-fig spp. in dry site; with non-figs in wet site	No	Patel 1997

No.	Study site (lat, long)	Forest type, elevation & annual rainfall	Years	Method, Species nos; individuals	Phenophases	Leaf flush/fall	Flowering peak	Fruiting peak	Climate variables	Reference
9.	Anamalai TR, Western Ghats, south India 10°25′N, 76°60′E	140-170 cm	Aug 1991-Jul 1993	Ten 1 ha plots, trails for fig trees; 19 genera; 652 trees	Unripe/ripe fruit	NA	NA	Feb-May		Kannan and James 1999
10.	Kangchup Hills, Manipur 24°45′ -24°51′N; 93°48′-93°53′E	Eastern Himalayan sub-tropical wet hill forest; 865 to 1785 m; 150 cm	Jan 1993 – Dec 1994	32; 160 trees	Monthly; Leaf fall, leaf flush, flowers, fruits	Mar-Apr; Aug-Sept	Major peak in Apr, minor peak in Sept	Overstorey spp.: Oct & Feb; Understorey spp.: Sept and Jan	No	Kikim and Yadava 2001
11.	Pakke TR, Arunachal Pradesh, north-east India, 27° 5′0″N, 92° 51′30″E	Tropical semi-evergreen forest; 100-1500 m; 170-300 cm	Feb 1997-Jul 2000	21 0.5 ha plots; 165 spp.; 1899 trees, GBH ≥ 30 cm	Monthly; young leaf, mature leaf, old leaf, leaf fall, flower, unripe, semi-ripe and ripe fruit	Not analysed	Wind-dispersed: bimodal Feb-Apr, Oct-Dec Bird-dispersed: No peak, uniform	Wind-dispersed: bimodal, Feb-Apr, Oct-Dec Bird-dispersed: May-July	Yes; rainfall, rainy days, min, max temperature, previous 6 months rain – described in Case Study section	Datta 2001 (unpublished thesis)
12.	Tunganath, Garwhal Himalaya, Uttarkhand, 30°14′N, 79°13′E	Alpine pasture; 3400-4400 m; snow-covered between Nov-April	1988-1998	171 spp.; 9% grasses, sedges, other monocots; 78% forbs; 13% shrubs, undershrubs	4-5 day intervals; propagule sprouting, seed germination, vegetative phase, flowering, fruiting, seed formation, senescence	NA	May-early Aug after snowmelt	June-Aug; declines in Sept-Oct; Senescence massive from Oct	No	Nautiyal et al. 2001
13.	Kalakad-Mundanthurai TR, southern Western Ghats, TN; 8°16'-30' -8°50'-30'N, 77°3O'-30' -77°15'-45'E	Wet evergreen forest, medium elevation; 150-340 cm	Apr 1991-Dec 1992	Transects; 60 spp.; 1269 orchids, herbs, shrubs, small trees	Monthly; flower, fruit	NA	Flower: Feb-Apr dry season; varied based on life-form	Fruit: July-Aug, wet season; varied based on life-form	Yes; rainfall -ve with overall flowering	Krishnan 2002

No.	Study site (lat, long)	Forest type, elevation & annual rainfall	Years	Method, Species nos; individuals	Phenophases	Leaf flush/fall	Flowering peak	Fruiting peak	Climate variables	Reference
14.	Goa state, northern Western Ghats; 15°48′N – 14°53′54″N; 74°20′13″ E-73°40′33″E	Several tropical forest types; 50 to 1100 m; 350 cm	Jan 1997-Jan 2000	113 endemic spp. including dicots, monocots – varied life-forms	Fortnightly/ monthly: only flowers	NA	Herbs: Sept Shrubs: Dec-Jan Trees: Feb-May Climbers: no distinct season, varies depending on habitat	NA	No	Joshi and Janarthanam 2004
15.	Kodayar, Tamil Nadu, Western Ghats, south India 77°15′E, 8°29′N	250-650 m; 234 cm	2 years, study years not given	42 spp.; 210 individuals; DBH ≥ 5 cm	Fortnightly; young leaf, mature leaf, leaf fall, flower bud, mature flower, flower fall, unripe/maturing/ripe fruit	Leaf fall: Dec to Jan (early dry season) Leaf flush: Feb to Mar	Flower bud: Jan-Apr	Unripe fruit: Mar-May Ripe fruit: May-July	Yes; rainfall, temp No correlation of leaf flush with both but with one month lag; flowering negative with rainfall but positive with min, max temp; ripe fruiting and rainfall positively correlated	Sundarapandian et al. 2005
16.	Kakachi, KMTR, Western Ghats, south India 8°33′N, 77°23′E	Wet evergreen forest; 1300 m; 300 cm	Mar 1991-May 1994	70 spp.; 300 individuals	Flowers, fruits	NA	Flowers: Feb-May and Sept		No	Ganesh and Davidar 2005

No.	Study site (lat, long)	Forest type, elevation & annual rainfall	Years	Method, Species nos; individuals	Phenophases	Leaf flush/fall	Flowering peak	Fruiting peak	Climate variables	Reference
17.	Hathinala forest, Vindhyas, Uttar Pradesh, north India, 24°18′N, 83°6′E	Northern tropical dry deciduous forest; 85 to 130 cm	May 2001 to Apr 2003	2 ha plot; 9 spp.; 90 individuals; tagged 160 twigs of 10 individuals	Leaf flush/leaf fall initiation and completion	Leaf flush: Mar-June Leaf fall initiation and completion: Nov-Mar	NA	NA	No	Kushwaha and Singh 2005
18.	Simlipal TR, Odisha, 21°28′ – 22°08′N, 86°04′ – 86°37′E	Tropical moist deciduous forest; 80 to 869 m; not clear	1 year; study years not given	Eight 1-ha plots; 90 spp.; NA	Leaf fall, leaf flush, flower, fruit	Leaf fall: Mar Leaf flush: Apr	Apr-May	May-June	No	Mishra et al. 2006
19.	Five sites in Coromandel coast, near Pondicherry, south India 11 to 13°N, 79 to 80°E	Tropical dry evergreen forest; 130 cm	Feb 2003 – Jan 2004	**22 spp.; 251 individuals GBH ≥ 10 cm	Monthly; Flower bud, open flower, immature, mature and fully ripe fruit	NA	Mar	Apr (dry) and Sept (wet)	No	Selwyn and Parthasarathy 2006
20.	Hathinala forest, Vindhyas, Uttar Pradesh, north India; 24°18′N, 83°6′ E	Northern tropical dry deciduous forest; 85 to 130 cm	May 2001-Jun 2003	2 ha plot; 9 spp.; 10 individuals (marked 4 branches, 160 twigs)	Monthly; Leaf flush initiation, completion; leaf fall initiation, completion; leafless period; initiation & completion of flowering; time lag between start of vegetative (first-leaf flush) & reproductive (first-visible flower) phases; initiation & completion of fruiting; fruit-fall initiation & completion	Duration of leaflessness related to flowering type. Varied from nil in Shorea to 200 days in Lannea, Boswellia that flower in dry season	Five flowering types; summer, rainy season, autumn, winter, dry season	Fruiting duration varied from 3 months in Shorea to 11 months in deciduous spp. like Diospyros that flower in summer	No	Singh and Kushwaha 2006
21.	Bala Fort RF, Aravalli Hills, NE Rajasthan 27°4′-28°4′N, 76°7′- 77°13′ E	Tropical dry deciduous thorn forest; 480-570 m; 70 cm	Jan 2001 –Dec 2003	Ten 100 m^2 quadrats; 26 spp.; not given	Fortnightly; Leaf flush/fall, flowers, fruits	Leaf fall: Oct–Dec	Leaf flush: Feb-May Mar-Apr; July-Aug	Sept-Oct	No	Yadav and Yadav 2008
22.	Kukkal, Palni Hills, southern Western Ghats;	Montane wet temperate forest; 1500-2450 m; 169 cm	Apr 2002-Apr 2004	6 ha plot; 23 spp.; 230 individuals	Young leaf, flower, fruit, unripe/ripe fruit	Data not presented	Data not presented	July	Yes, Fruiting with rainfall (+ve)	Somasundaram and Vijayan 2010
23.	Three sites in the Nilgiri hills; 11°43′N, 76° 87′E, 11°2′N, 76°87′E, 11° 24′N, 76°56′E	Shola montane forests; 2100 -2300 m	Aug 2000-Aug 2003	Transects;70 spp.; 500 trees	Leafless, leaf flush, expanding, mature leaf, senescent leaf	Leaf flush: Feb-Apr Leaf expansion: Apr-May Leaf fall: Dec-Jan	NA	NA	Yes; Leaf flush: -ve soil moisture, rainfall, Leaf expansion: +ve sunshine hours, max temp, Leaf fall: -ve, soil moisture, max temp	Suresh and Sukumar 2018
24	Katerniaghat Wildlife Sanctuary	Moist deciduous forest	2009-2010	Selection on basis of size class, 2 spp. (Shorea robusta and Ficus hispida), 20 individuals	Time of leaf emergence, leaf area, leaf fall, flower and fruit initiation	Leaf initiation (Shorea/Ficus) – Mar/Apr,	Flower bud initiation – Mar,	Fruit (Shorea) – May, Syconium initiation (Ficus) - Apr	Temperature, precipitation, day length	Bajpai et al. 2012
25	Bhadra Wildlife Sanctuary 13°25′ and 13°50′ N, 75°15′ and 75°50′ E	Dry deciduous; evergreen	2004-2006	Transect, 22 spp. and 157 trees in dry deciduous site; 17 spp. and 66 trees in evergreen site, percentage classes - canopy with phenophase	Leaf initiation, leaf expansion, leaf fall	Dry deciduous : Leaf flush – starts Feb and peaks in Apr, Leaf expansion – starts in Feb and peaks in July, Leaf fall – peaks in Jan Evergreen: Leaf initiation – peaks in Oct, Leaf expansion – Jan	NA	NA	Rainfall	Nanda et al. 2013

No.	Study site (lat, long)	Forest type, elevation & annual rainfall	Years	Method, Species nos; individuals	Phenophases	Leaf flush/fall	Flowering peak	Fruiting peak	Climate variables	Reference
26.	Pakke TR, Arunachal Pradesh, north-east India, 27° 5′0″N, 92° 51′ 30″E	Tropical semi-evergreen forest; 100-1500 m; 170-300 cm	1997-2000; 2009-2012	Single spp.: Horsfieldia kingii 1997-200:6 trees; 2009-12: 24 trees	Flowers, unripe fruit, ripe fruit Presence/ absence: 0,1	NA	Apr-July; variable between years; supra-annual	Feb-May; Peak: Feb-Mar; Varied from 0 to 33% of trees	Yes but not used in study	Datta and Rane 2013
27.	Hollongapar WLS, Assam, north-east India; 26°40″ to 26°45″N and 94°20″to 94°25″E	Tropical semi-evergreen; 100-120 m	Apr 2010-Mar 2012	Single spp. –Vatica lancaefolia, 25 trees; GBH ≥ 40 cm	Monthly; leaf abscission or senescence of leaves, leaf flushing, flowering, fruiting, fruit fall and vegetative growth	Leaf abscission, flush: Dec	Mid-Apr-May	May-June Fruit fall: July	Weather data recorded but not used in analysis	Borah and Devi 2014
28.	Bhadra WLS, Karnataka, south India 13°46′ - 13°52′ N, 75°36′ -75°42′E	Tropical dry deciduous; 690-750 m; 10 to 55 cm Evergreen; 500 - 2000 m, 48 to 150 cm	Jun 2004 - May 2006	Site 1: 45 spp., 277 trees; Site 2: 47 spp., 177 trees	Leaf bud /leaf initiation, leaf expansion and leaf fall / leaf senescence	Site 1 Leaf flush Apr Leaf fall: Jan Site 2 Leaf flush: Jan Leaf fall: Feb	NA	NA	Yes, rainfall, min and max temperature, Leaf flush and leaf senescence –ve rainfall, min temp, rainy days; Leaf expansion +ve max temp, -ve with rainfall	Nanda et al. 2015
29.	Chatla floodplain, Cachar district, Assam 90°45′E and 24°45′N	Low-lying floodplain forest; 180-250 cm	June 2012-May 2014	Single spp. – Barringtonia acutangula; 40 trees	Fortnightly; Leaf flush/fall; flower, fruit	Leaf flush: Mar-Apr Leaf fall	May-June	July-Aug	Yes, rainfall, temperature +ve with flowering, fruiting	Nath et al. 2016

No.	Study site (lat, long)	Forest type, elevation & annual rainfall	Years	Method, Species nos; individuals	Phenophases	Leaf flush/fall	Flowering peak	Fruiting peak	Climate variables	Reference
30.	Katerniaghat WS, Uttar Pradesh, north India; 27°41′–27°56′ N and 81°48′ –81°56′E	Tropical moist deciduous forest; 116 to 165 m; 60 to 65 cm	Nov 2009 – Oct 2012	8 spp.; 80 individuals, tagged 160 twigs of 10 individuals	Monthly; leaf flush, leaf fall, flower bud, mature flower, unripe/ripe fruit	Leaf flush: Feb-Apr Leaf fall: Nov-Mar	Feb-April (dry season)	Mar-June (before rainy season)	Monthly Temperature, rainfall, humidity, day hours, shown graphically with phenophases	Bajpai et al. 2017
31.	Gorakhpur Forest Division, Uttar Pradesh; 27° 05′ - 27° 40′N, 83° 30′ - 84° E	Tropical moist semi-evergreen forest; 95 m; rainfall not given	One year; study year not given	Single spp. – Trewia nudiflora, 6 to 12 individuals	Leaf flush, leaf fall, flower bud, mature flower, unripe/ripe fruit	Leaf flush: Feb-Aug Leaf fall: Oct-Dec	Dec to June Variable depending on sex of tree and elevation	Apr-Aug	Yes; light intensity, soil moisture information collected but not correlated	Chaurasia and Shukla 2016
32.	Mudumalai TR, Tamil Nadu, south India 11°30′-11°39′N, 77°27′ - 77°43′E	Tropical dry deciduous; 1000 m; 110 cm	Aug 2000-2008	Transect; 3 fig spp.; 11	Monthly; leaf flush, fall, unripe and ripe syconia	Leaf flush: Feb-Apr Leaf expansion: Feb-July Leaf fall: Dec-Feb	Initiation: Jan-Sept Peak: July	Maturation peak: Sept-Oct (wet season)	Yes; rainfall, min & max temp, soil moisture, sunshine hours	Suresh and Sukumar 2018
33.	Pakke TR, Arunachal Pradesh, north-east India, 27° 5′ 0″N, 92° 51′ 30″E	Tropical semi-evergreen forest; 100-1500 m; 170-300 cm	Aug 2009-ongoing	Trails; 54 spp.; 716 trees; analysis mainly for 39 spp. with > 4 individuals, GBH ≥ 30 cm	Fortnightly; young leaf, mature leaf, old leaf, leaf fall, flower bud, flower, unripe, and ripe fruit Presence/absence: 0,1 Scoring only for URF/RF: 0-4, (0, 1= >0-25%, 2 = >25-50%, 3 = >50 - 75%, 4 = >75 -100% of canopy	Leaf flush: mainly Apr – Aug (in terms of no. of spp.)	Mar to May (no. of spp.) Wind-dispersed: Mar-May; Oct-Nov; Bird-dispersed: Apr-June	Wind-dispersed: Feb-Apr; Bird-dispersed: Mar to May Quantum of fruiting low – up to 15% of trees only	Temperature rainfall, humidity, solar irradiance, pressure, wind speed; analysis ongoing	Datta et al. (unpublished data)

No.	Study site (lat, long)	Forest type, elevation & annual rainfall	Years	Method, Species nos; individuals	Phenophases	Leaf flush/fall	Flowering peak	Fruiting peak	Climate variables	Reference
34.	Rishi Valley, Andhra Pradesh, 13.6363° N, 78.4539° E	Semi-arid, predominantly scrub	Dec 2007-ongoing	Opportunistic; 15 spp. with 40 individuals each; 3 spp. with < 11 trees	Fortnightly; Leaf flush, Mature leaves, Flower bud, Flower open, Unripe fruit, Ripe fruit 0-2, (0, 1 = >0 to 33%, 2 = >33% - 100%)	Leaf flush: Mar-Oct peak in Jun Leaf fall: Jan-Apr. Peak in Mar	Flower bud: Feb-Sept Peak in May Mature flower: Mar-Oct Peak in May	Fruit: May-Jan. Peak in Oct	Temperature, rainfall, photosynthetically active radiation, wind speed, wind direction recorded; analysis partially completed – Shrubs leaf flush, flowering +ve rainfall. Trees leaf flush +ve rainfall and temperature, flowering +ve temperature	Quader et al. (unpublished data)
35.	Nigdale Maharashtra, northern Western Ghats 19°4′N 73°33′E	Seasonally dry tropical forest; 900 m; 226 cm	2014 - ongoing 6 years for 24 spp.; 4 years for 79 spp.	79 woody spp., 1600 trees (15-30 individuals per sp)	Monthly; leaf flush, leaf senescence, flowering, fruiting;	Leaf flush coincides with max light availability; deciduous spp. flush close to onset of rains	Analysis underway	Analysis underway	No	Barua et al. (unpublished data); Chakrabarty and Barua 2018
36.	Anamalai T, Western Ghats, Tamil Nadu, 10°25′01″N, 77°03′24″E	Tropical evergreen forest; 600-1400 m	Mar 2017 - ongoing	7 trails; 173 spp.; 1808 trees in total; 1584 trees monitored	Monthly: Leaf flush, mature leaves, fallen leaves, flower buds, open flowers, unripe fruits and ripe fruits 0-4; 0, 1= 0-25%; 2 = 25-50%; 3 = 50-75%; 4 = 75-100% of the canopy	Analysis underway	Analysis underway	Analysis underway	Temperature, rainfall, Photosynthetically active radiation, wind speed, wind direction recorded	Srinivasan et al. (unpublished data)

*Data only analysed for 13 species for which a minimum of five individuals were observed.

**Phenology had been recorded for 84 species (shrubs, lianas and trees) for flowering and fruiting but detailed data was collected for 22 woody species.

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