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Introduction

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Climate change and ecosystems: threats, opportunities and solutions

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The rapid anthropogenic climate change that is being experienced in the early twenty-first century is intimately entwined with the health and functioning of the biosphere. Climate change is impacting ecosystems through changes in mean conditions and in climate variability, coupled with other associated changes such as increased ocean acidification and atmospheric carbon dioxide concentrations. It also interacts with other pressures on ecosystems, including degradation, defaunation and fragmentation. There is a need to understand the ecological dynamics of these climate impacts, to identify hotspots of vulnerability and resilience and to identify management interventions that may assist biosphere resilience to climate change. At the same time, ecosystems can also assist in the mitigation of, and adaptation to, climate change. The mechanisms, potential and limits of such nature-based solutions to climate change need to be explored and quantified. This paper introduces a thematic issue dedicated to the interaction between climate change and the biosphere. It explores novel perspectives on how ecosystems respond to climate change, how ecosystem resilience can be enhanced and how ecosystems can assist in addressing the challenge of a changing climate. It draws on a Royal Society-National Academy of Sciences Forum held in Washington DC in November 2018, where these themes and issues were discussed. We conclude by identifying some priorities for academic research and practical implementation, in order to maximize the potential for maintaining a diverse, resilient and well-functioning biosphere under the challenging conditions of the twenty-first century.

This article is part of the theme issue 'Climate change and ecosystems: threats, opportunities and solutions'.

1. Introduction

Changes in the atmosphere and oceans can profoundly change the biosphere, the thin living film of life on Earth that is intrinsically coupled to the atmosphere and hydrosphere and provides the nourishing fabric within which human societies exist. Hence, degradation or restoration of parts of the biosphere are likely to have regional or planetary consequences. Anthropogenic greenhouse gas emissions, which drive both climate change and ocean acidification, increasingly threaten the viability and resilience of natural ecosystems, and the human societies that depend upon them. The effects of these threats can be profound and, in recent years, have become increasingly observable. Already, Earth is committed to a substantially warmed climate, with expectations of further warming into the future, unless carbon emissions trajectories change dramatically (https:// www.ipcc.ch/report/srccl/) [1].

Scientific research continues to refine the understanding of Earth's climate system and its interdependence on the biosphere. For the most part, projections indicate an increased likelihood of negative consequences of climate change for ecosystems and people. Indeed, climate-related impacts are already being witnessed and seem to be increasing in severity and frequency. A number of potential climate tipping points in the Earth system are already showing early signs of activation [2]. Consequently, the 2018 International Panel on Climate Change (IPCC) Special Report on 1.5°C (https:// www.ipcc.ch/sr15/) warns that allowing the planet to warm beyond 1.5°C will result in climate change impacts, including drought, floods, heat waves and sea-level rise, that are deleterious for humanity and for biodiversity. While the previous internationally agreed target was 2°C, this half-degree difference could reduce the risk of extensive degradation of Arctic and coral reef ecosystems. A 1.5°C maximum warming ambition implies that the world has about 12 years to reduce global net carbon emissions by half to avoid the most significant impacts, but even if this target is achieved, potential impacts of warming are likely to continue for decades or even centuries [3].

In this thematic issue, we present contributions that culminate from discussions held at the 2018 Royal Society-National Academy of Sciences Forum on Climate Change and Ecosystems. The aims of the Forum, jointly organized by the two societies, were to build new opportunities for international collaboration, highlight the latest research findings on the focal topic, identify research gaps and future research priorities and discuss how research in this field may inform international policy [4]. The Forum examined the latest science on how climate change can affect terrestrial, aquatic and marine ecosystems, often in interaction with other factors. In particular, it addressed research frontiers such as the effects of changes in climate variability and extremes; interactions among multiple stressors; thresholds and the potential for abrupt change; and multi-trophic interactions, across a range of terrestrial, aquatic and marine ecosystems. The Forum also considered opportunities to assist and manage ecosystems to enhance both their resilience and societal resilience to climate change by exploring a range of science and policy dimensions. This included how ecosystems can best be managed to enhance their resilience to climate change, their ability to transform under climate change and how ecosystem management can be a strategy for more general adaptation to change. Hence, a central focus was to consider how ecosystem management and restoration have the potential to contribute 'nature-based solutions' (NbS) to tackle both the causes and consequences of climate change. However, the effectiveness, scalability and magnitude of different nature-based strategies need to be explored, better understood and evaluated [5].

The resulting thematic issue, and our introduction to it, are organized around (i) the threats that climate change poses to ecosystems, (ii) the opportunities to enhance ecosystem resilience to climate change, and (iii) the consideration of how ecosystems and ecosystem restoration can assist climate change mitigation and adaptation. In our introduction we outline the themes, introduce the papers in the thematic issue, and conclude with a synthesis of the main findings of the Forum. In doing so, we emphasize the research needed to better understand threats, opportunities and solutions regarding climate change and ecosystems.

2. Theme 1: climate change threats and challenges to ecosystems

The Forum examined several aspects of the latest science on how climate change affects terrestrial, freshwater and marine ecosystems, often in interaction with other factors. In particular, it explored current research frontiers including the effects of change in climate variability and extremes; interactions of climate change with other human-induced stressors; thresholds and the potential for abrupt and irreversible change; and multi-trophic interactions. Ecosystems are rapidly changing in response to climate change and other global change drivers, not only in response to temperature changes but also associated changes in precipitation, atmospheric carbon dioxide concentration, water balance, ocean chemistry, and the frequency and magnitude of extreme events. Ecosystems vary in their sensitivity and response to climate change because of complex interactions among organisms, disturbance and other stressors.

Changes in natural ecosystems threaten biodiversity worldwide, and have implications for global food production. The papers in this section advance our thinking about the effects of climate change on ecosystem properties (biological diversity, trophic webs or energy flux, nutrient cycling or material flux) in different ecological communities (terrestrial plants, invertebrates in marine sediments, terrestrial soil microbes).

In the opening paper of this section, Turner *et al.* [6] link climate variability and extremes to the potential for sudden and irreversible changes in ecosystems. Abrupt changes in ecological systems (ACES) are difficult to observe empirically because extreme events are, by their nature, stochastic and seldom predictable. Nonetheless, the authors urge scientists to make detecting, explaining and anticipating ACES in response to climate change a high priority. There is no 'new normal' (equilibrium), rather we are beginning to witness accelerating rates of change in the intensity and frequency of specific drivers. The study identifies important generalities that lead to questions and hypotheses for future research. These are: some dimensions of ecological systems are more prone to abrupt change than others; climate extremes may be more likely than mean trends to trigger abrupt change (e.g. coral bleaching is driven by extreme heatwaves rather than gradual ocean warming); multiple drivers often interact to produce ACES (e.g. climate change-driven drought and extreme fire can lead to abrupt changes of terrestrial ecosystems from forest to non-forest, introduced pathogens in combination with climate can cause populations of sensitive species to crash); historical contingencies (ecological legacies, frequency and order of disturbance, spatial context) are important drivers of ACES owing to ecosystem memory; and strong positive feedbacks in an ecosystem can sometimes lead to persistent state changes at critical transitions (tipping points).

Climate extremes and historical contingencies are also considered by Bardgett and Caruso [7], who synthesize current understanding of the attributes of belowground ecological communities that make them resistant, resilient or vulnerable to climate extremes. Soil microbial communities play a critical role in mediating biogeochemical cycling. Key intrinsic attributes of these communities that confer resilience include life-history strategy (growth rate, resource use efficiency) and microbial food web diversity (fast and slow energy channels found in bacterial versus fungal food webs). Fast energy channels (e.g. bacteria in a soil context) rapidly recycle nutrients and recover quickly from disturbances, hence providing resilience to change, whereas slow energy channels (e.g. fungi) cycle nutrients slowly, dampen responses to perturbations and hence confer resistance to change. The complementary functions of these two energy channels can facilitate rapid yet stable recovery from perturbations, and, conversely, alteration of the relative influence of these channels can destabilize an ecosystem. Extrinsic attributes include environmental variability, and the contributions that the plant community make to soil carbon, moisture and nutrients. While the response of belowground communities under chronic stress is fairly well understood, the authors identify response to climate extremes, and potential for abrupt ecological change, as critical knowledge gaps that should be addressed experimentally.

Resilience in ecological communities requires longer-term perspectives to improve our understanding of community responses to change. Iglesias and Whitlock [8] use palaeoenvironmental records of pollen and charcoal from temperate forests in the Northern and Southern Hemispheres to consider the role of fire in changing forest tree species composition. They find that the resilience or vulnerability of forest species composition to changing fire regimes depends on a variety of local factors, including climate, soil conditions and historical legacies; in some cases, extreme events, combined with biophysical feedbacks, can cause ecosystems made up of long-lived species to completely shift in ecosystem composition in response to a single fire event. Temperate forests have undergone both long periods of stability and abrupt change in response to climate change and human activities (burning for land clearing) during the Late Quaternary, and a site-specific understanding of stability versus disequilibrium is needed to anticipate future ecological scenarios under rates of warming that are unprecedented in the Holocene and beyond.

Climate change ultimately drives terrestrial biodiversity loss and affects ecosystem carbon storage both directly and indirectly via land use change, i.e. climate change-driven cropland expansion. Molotoks *et al.* [9] use a modelling approach to explore uncertainties in projections of biodiversity and carbon loss and find that, in spite of large uncertainties associated with land use projections, future cropland expansion is likely to have negative impacts on biodiversity and carbon storage in many biodiversity hotspots, including Mexico, Amazonia and the Congo Basin. This work highlights the importance of including indirect effects via changes in land use when assessing the total biodiversity and carbon impacts of climate change.

We close this section of the thematic issue with a thought-provoking essay by Harrison [10], which predicts that terrestrial plant community diversity will be eroded more than it is enhanced by climate warming, and calls for experimental work to test this prediction. She warns that current evidence suggesting climate warming might generally enhance diversity in temperate latitudes may not be generalizable because a preponderance of studies has occurred in the particular and unusual context of north-temperate alpine ecosystems. She predicts that net loss of diversity will predominate in water-limited ecosystems; losses will also occur in temperature-limited systems without steep topographical gradients where pools of potential replacement species are not found nearby.

3. Theme 2: opportunities to improve resilience to climate change

The scientific understanding of the opportunities to assist and manage ecosystems in order to enhance ecological and/or societal resilience to climate change and ocean acidification, including novel conservation and restoration approaches, was a key consideration of the forum.

First, Thomas [11] provides a novel view of biodiversity conservation in a world where the biosphere is profoundly transformed by human action. Fundamental biological processes, unchanged by human action, form a framework for understanding the ecosystem response to global change where human actions rapidly remove, add and move around species, populations and genes. These evolutionary and ecological processes continue to operate in a human-altered world where novel ecological communities consist of species, populations and genes that are well matched to the human-altered environment. He argues, provocatively, that facilitating, rather than repelling the arrival of new species and genes that provide benefits is a legitimate conservation strategy in the Anthropocene. He advocates greater emphasis on connectivity or '*trans situ*' conservation, enabling species and genes to reach locations where they might thrive despite the challenges of a rapidly changing world.

The effects of climate change are often most damaging through changes in the intensity and frequency of extreme events rather than through changes in mean conditions (as argued by Turner *et al.* [6]). Franca *et al.* [12] review the effects of climate extreme events (storms, floods, heatwaves, droughts) on post-disturbance ecosystem recovery in high-biodiversity tropical ecosystems, providing a novel synthesis across coral reef and tropical forest ecosystems. They demonstrate that climate extremes interact synergistically with local anthropogenic disturbances and mean climate trends, and conclude that all three of these drivers of biodiversity loss must be addressed for effective conservation management. Local actions to protect or restore ecosystem complexity and structure can increase resilience to extreme events: they highlight examples of key multi-trophic animal-mediated processes (seed dispersal by dung beetles, grazing by parrotfish) that assist ecosystem recovery in tropical forests and coral reefs.

Most of the literature on nature-based approaches to climate mitigation and adaptation has tended to focus on purely terrestrial ecosystems (e.g. forests and peatlands) or terrestrial-coastal systems (e.g. mangroves and salt marshes). By contrast, Solan *et al.* [13] examine the climate mitigation and adaptation potential of marine benthic soft-sediment ecosystems. These are the most extensive habitat on Earth, can host high levels of biodiversity, and benthic fauna and flora can play key roles in regulating biogeochemical cycling, climate-active gases, ocean chemistry and the long-term removal of carbon from the ocean-atmosphere system. The particle reworking and ventilatory behaviour of sediment-dwelling invertebrates can significantly exacerbate, buffer or alleviate the effects of warming, acidification, deoxygenation and sea-level rise. Interest in climate change adaptation is driving interest in benthic habitat restoration, but the science is in its infancy. As with coral reefs [12], direct disturbance of such systems (e.g. through bottom-trawling) can interact with responses to climate extreme events. Conversely, strategic protection of key areas in a network can enhance wider, seascape scale resilience and ecosystem function. Network connectivity of benthic protected areas is a key factor in conferring wider-scale climate change resilience, but questions remain about how to achieve scalable benthic-based mitigation measures.

Similarly, Roberts *et al.* [14] highlight the potential synergies between marine biodiversity protection and the mitigation of, and adaptation to, climate change. Protection often strengthens the capacity of ecosystems to retain carbon, and in some cases continue to sequester additional carbon, as well as enhances ecological resilience to climate change. However, much of what we know about the links between ecosystem intactness and carbon sequestration emanates from terrestrial ecosystems. Marine ecosystems, where conserved fish and marine mammal populations may enhance the ocean nutrient cycle and associated sequestration rates, are less appreciated. Recent work, for example, has highlighted the role of marine megafauna in enhancing vertical nutrient transfer (cetacean deep-feeding, surface defecation and physical mixing), thereby modifying ocean fertility and carbon sequestration at large scales. The authors call for an expansion of marine protected areas from the current 10% of sea area in the Aichi targets, to 30% of sea area to accommodate such phenomena.

Lawler *et al.* [15] also consider optimal protected area network connectivity in the face of climate change, estimating the cost of the configuration of a terrestrial conservation network for the conterminous United States (US) that considers both current and projected distributions of biodiversity under climate change scenarios. They discover that the configuration of the protected area network changes substantially under consideration of climate change, and that the additional cost of planning for climate change may be relatively modest compared to the cost of expanding the reserve network without considering climate change. In particular, protecting some kinds of climate refugia may be an inexpensive conservation strategy. They also note that the higher elevation bias of protected areas in the US, that has been seen as problematic for conservation, may provide benefits in the face of climate change by protecting climate refugia.

4. Theme 3: solutions and practical applications

Our final focus is on the opportunities and challenges associated with the practical management, restoration and protection of ecosystems to support climate change mitigation and adaptation interventions. The potential to protect, restore and use ecosystems as tools to tackle climate change has gained increasing traction under the broad/overarching framework of NbS, or 'natural climate solutions' (NCS) where the context is mitigation of climate change [16]. NbS can make a partial contribution to slowing and limiting global warming, while also potentially supporting biodiversity and ecosystem services, if 'maladaptive' NbS, such as non-native monoculture plantations, are avoided. Seddon *et al.* [17] present an overview of the concept of NbS and its increasing prominence in international policy. They present a new conceptual framework clarifying the role of NbS in integrating the ecosystem with the socioeconomic system, and illustrate how, with careful and equitable implementation, NbS can reduce the vulnerability of the social–ecological system as a whole. They highlight key evidence for nature's role in reducing social–ecological vulnerability and sensitivity to climate change impacts, as well as cases where NbS enhance the adaptive capacity of both ecosystems and societies. Seddon *et al.* [17] also discuss some of the major challenges in evaluating the effectiveness of NbS, as well as the financial and governance obstacles to implementation at scale.

As ecosystems transform under climate change, so does their capacity to support human adaptation (i.e. to provide so-called 'adaptation services'). In their article, Lavorel *et al.* [18] set out to operationalize the concept that humans and ecosystems 'co-produce' these services. They take the novel approach of analysing the co-benefits, trade-offs and synergies among different adaptation services along an ecosystem cascade involving ecosystem management, mobilization, appropriation, social access and appreciation. Using five case studies across a range of socio-ecological systems they demonstrate how broad mechanisms can enhance co-benefits and minimize trade-offs between adaptation services. They conclude by arguing that awareness of such co-production mechanisms will enable proactive management and governance for collective adaptation to ecosystem transformation.

Soto-Navarro *et al.* [19] present a detailed spatial analysis of the congruence between the carbon storage value of ecosystems and their biodiversity value. Whereas carbon value is essentially unidimensional, biodiversity value can be more challenging to map as it contains many dimensions and is geographically contingent. For instance, a tropical forest generally has much more species richness than an Arctic ecosystem, but the latter has unique biodiversity value. Using multiple indices, they assemble maps of both the proactive biodiversity conservation potential (areas of high-biodiversity intactness which are not under immediate threat but could benefit from proactive protection) and areas of reactive conservation priorities which are under immediate threat. The study highlights where biodiversity and carbon priorities converge (e.g. tropical and boreal forest regions) versus where they diverge (e.g. grasslands), where a focus on carbon and climate mitigation may not deliver biodiversity benefits and, in many cases, may be detrimental to local biodiversity (e.g. through carbon-focused afforestation of natural grasslands).

The national potential for NCS in tropical countries, where the carbon sink provided by forests is significant and there is the greatest potential to mitigate climate change through NCS, is evaluated by Griscom *et al.* [20]. They consider not only protection and restoration of forests but also of other native ecosystems, such as peatlands and mangroves, as well as improved management of working lands. Twelve NCS pathways are considered that could deliver significant climate change mitigation and provide biodiversity benefits and other ecosystem services, primarily by avoiding forest conversion. A small group of countries harbours the majority of tropical NCS potential, and all but one of them has above-average metrics for governance, indicating feasibility and capacity for implementation of NCS using protect-manage-restore strategies.

Hobbie and Grimm [21] focus on the potential of ecosystem-based approaches to climate change adaptation in urban contexts. By 2050, around two-thirds of humanity will be urban dwelling, and cities will be a major nexus for climate change impacts and adaptation. Many features of cityscapes make them particularly vulnerable to climate change hazards, including low vegetated cover, high impervious cover, generation of pollutants, heat island effects, high demand for fresh water resources, and concentration of population and infrastructure in vulnerable areas such as coastal zones, river floodplains and deforested hillsides. Nature-based strategies can mitigate climate change hazards, and the amplifying effects of urban areas on those hazards. These strategies include enhanced vegetation cover and green space, construction of structures that restore natural hydrologic function such as stormwater ponds, bioswales, green roof and riparian zones; and restoring natural protective habitats along coastlines. A full assessment of these nature-based strategies does, however, need to assess the costs (including negative impacts) of these strategies compared to technical approaches.

Sandom *et al*. [22] examine trophic rewilding as a management strategy for restoring ecosystems that may also contribute towards mitigating climate change. Humans have dramatically changed ecological assemblages of large-bodied herbivores and predators over the past 50 000 years. In many parts of the world large, non-ruminant herbivores have been eliminated and replaced by domestic ruminant grazing livestock, resulting in dramatic changes in vegetation structure, fire regimes and biogeochemical cycling, including the carbon cycle. Scenarios in which rewilding replaces ruminant livestock with extant native herbivores would reduce methane emissions (a powerful greenhouse gas), but whether it would have a net mitigating effect on climate change would vary among regions of the globe owing to variation in effects extant native herbivores have on fire and woody vegetation dynamics among those biomes. They conclude that rewilding for the purpose of restoring ecosystem complexity and biodiversity does not aim to deliver specific benefits, and that scenarios using extant native herbivores are unlikely to maximize NCS, but can provide a broad range of ecosystem and biodiversity benefits.

Macias-Fauria *et al*. [23] explore the science and potential of a specific and somewhat unconventional but striking megafaunal approach to climate change mitigation: the introduction of grazing and browsing megafauna (horses, bison, cattle) to Arctic high boreal and tundra regions. Such introduction may facilitate the restoration of the ‘mammoth steppe,’ an extensive high-latitude grassland biome that it is argued was lost with the extinction of the high-latitude Pleistocene megafauna, to which the arrival of human hunting cultures is likely to have substantially contributed. Such high-latitude grassland ecosystems may delay and reduce the risk of permafrost degradation and a resulting surge in carbon and methane emissions in a warming Arctic, and thereby contribute to limiting the risk of a dangerous climate change positive feedback in the Arctic permafrost. The authors highlight that, while plausible, much of the science remains untested, but that such ‘land use’ options in the Arctic may be as influential on climate as much more studied impacts of land use on climate in mid- and low-latitudes. As with other forms of NCS, the challenge of implementation at sufficient scale to make a significant difference to global climate remains daunting.

The final two papers in this themed issue [24,25] address the challenge of scalability and societal transformation: how can changes in ecosystem management and restoration be implemented at sufficient scale to achieve meaningful climate change mitigation and adaptation, while also protecting biodiversity? Norton *et al*. [24] explore the potential of scaling up NbS through public social assistance schemes for employment, whereby payment is given to poor or vulnerable groups in return for employment in public works. With reference to well-established large-scale public works programmes in India, Ethiopia and Mexico, they discuss the potential of incorporating labour-intensive NbS, such as reforestation, into these schemes. They conclude that to realize the potential of employment-based social assistance for ecosystem benefits, the design and maintenance of local public works must be strengthened so as to better support biodiversity (e.g. through ecosystem restoration).

Finally, Lenton [25] argues how, in the Anthropocene, tipping points in ecological and climate systems are becoming deeply intertwined and tightly coupled with socioeconomic and technological systems. He discusses the urgent need to identify and trigger positive tipping points towards global sustainability. And he presents evidence of how our considerable knowledge of the dynamics of environmental tipping points, including identification of early warning signs and of the conditions needed to trigger cascades of change, could and should be used to inform the deliberate tipping of positive change in human societies.

5. Summary

(a) Understanding threats and challenges to ecosystems

To date, climate change has had a relatively modest effect on ecosystems and biodiversity, compared to direct anthropogenic actions such as overharvesting and land use change resulting in habitat loss. This relative importance is already changing, and the negative ecological impacts of climate change are becoming more apparent and very likely to intensify over the coming decades (e.g. [26–28]). On land, climate change is increasing precipitation variability and the probability of extreme dry and wet events, and long-term warming and increasing atmospheric water deficits are increasing physiological and hydrological stress and ecosystem flammability. In the ocean, an increased occurrence of heatwaves and long-term trends of acidification increase physiological stress on many organisms and ecosystems. Interaction of other anthropogenic stressors such as defaunation, overfishing, invasive species, fragmentation and direct habitat degradation tend to amplify the sensitivity of ecosystems to climate change. It is extremely challenging to predict the patterns and probabilities of biodiversity loss, both from the subtle effects on individual species within complex multi-trophic ecosystems and the more abrupt effects of ecosystem degradation.

In the context of the complexity of ecosystems and a vast shortfall in the understanding of how specific species, and interspecific interactions, will respond to climate change, there is a need to adopt a strategy of adaptive ecosystem research, in addition to adaptive ecosystem management. There are many aspects of ecosystem science where we will not know enough in sufficient time. Ecosystems are changing so rapidly in response to global change drivers that our research and modelling frameworks are overtaken by empirical, system-altering changes. New frameworks for modelling and monitoring highly dynamic complex systems need to be applied. We need improved ways to implement adaptive ecosystem management under uncertainty.

Long-term monitoring plays an essential role too. It can provide insights into long-term shifts that are difficult to register because of shifting baselines, and provide early warning of species-specific vulnerability or ecosystem-wide decline or tipping points. As examples, long-term forest monitoring has provided important evidence about the biosphere carbon sink which helps slow down the rate of climate change, and its potential future pathway [29]. With a few notable exceptions, long-term monitoring is extremely challenging to fund in an environment of short funding cycles, yet such ecological 'weather stations' are essential if we are to understand and mitigate the changes that are underway in the biosphere. Imagine where climate change science would be if routine monitoring of the weather had not been widely adopted in the twentieth century.

(b) Opportunities for improving ecosystem and societal resilience

Ecosystems play an active role in the climate system, especially through their role in the carbon cycle, the water cycle and other biogeochemical cycles. If sustainably managed in a way that draws on robust ecosystem and biodiversity science, ecosystems can be a major source of human resilience and can support the adaptation of human societies to rapid environmental change. In other words, ecosystems are not merely vulnerable to climate change, but have the potential to be significant allies in the challenges of climate change adaptation and mitigation.

Ecosystems have complex responses to climate change, which are incompletely understood and only partially incorporated into future projections of ecosystem function and dynamics. In many cases, this complexity could act as a cushion and needs to be better understood, e.g. habitat heterogeneity can provide micro-islands of resilience that can be sources of recovery following extreme events, and genetic variability can allow resilient subpopulations to adapt and expand. Multi-trophic interactions and trophic redundancy may help ecosystems recover from a disturbance in biodiversity hotspots. Strategic protection of key areas in a protected area network, those that support biodiversity under current and future climate, can enhance the wider landscape and seascape scale resilience and ecosystem services, including those mitigating climate change (e.g. carbon sequestration).

(c) Nature-based solutions

Rather than being framed as a victim of climate change, biodiversity can be seen as a key ally in dealing with climate change. Ecosystem management and careful evidence-based restoration and stewardship have the potential to play major roles in climate change mitigation and adaptation. However, ecosystem-based solutions will be far from sufficient and there is still an urgent need to address the fossil fuel emissions problem as the primary approach to halting climate change. On the other hand, NbS often have many co-benefits to human societies. The contributions to this issue have illustrated these co-benefits e.g. urban ecosystems, tropical forests and high-latitude biomes, using strategies that range from restoring hydrologic function, to forest protection and restoration, to trophic rewilding. These papers have also shown that some maladapted ecosystem-based climate mitigation actions (e.g. large-scale bioenergy, afforestation of natural grasslands and peatlands) could have negative effects on terrestrial biodiversity and resilience [30]. There remains a need for better understanding of the benefits of NbS for fisheries, agriculture and other ecosystem services to human society, including how ecosystem management of multiple ecosystem services can also contribute to climate change mitigation [17]. Such a synthesis of evidence needs to evaluate the challenge of under-reporting of negative results, which can lead to an inflated assessment of the effectiveness of specific approaches and methodologies. It also needs to extend such analysis to a wider range of habitats and ecosystems [13], and evaluate the effectiveness of NbS using multiple response variables over appropriate spatial and temporal scales. There is already a growing evidence base for NbS to climate change mitigation and adaptation, which generally shows they are effective but more emphasis is needed on identifying their limits and challenges. This evidence is not sufficiently disseminated to inform decisions at all levels from international to local [17].

A major challenge in understanding and implementing nature-based approaches to climate change adaptation and mitigation is that of scalability. Climate change is a global problem, requiring multi-jurisdictional and multinational governance, yet many of the examples of NbS concern proof of concept studies over relatively small spatial scales. Additional benefits of solutions can be quite significant and may overcome the opportunity costs. The costs and benefits of solutions, as well as the problem itself, are inequitable across social groups. How can institutions be designed so that those who benefit are empowered to implement management actions? If the global community invests in local solutions in poor communities, there can be local and global benefits. There may be innovative opportunities for scaling, e.g. working with existing rural social protection programmes [24], or local fisheries management programmes, and many examples of good practice are emerging [5].

(d) What role for academic research?

A broad spectrum of academic research can contribute to understanding ecosystem responses to climate change, and facilitate ecosystem-based adaptation and mitigation. In terms of *ecological science*, there is an abundant need to understand how ecological systems function, how they are changing and will continue to change under environmental conditions with no historical analogue, and what interventions are needed to maintain and restore ecosystems. In terms of *environmental economics*, there is a need to understand the costs and benefits of any intervention, and how those costs and benefits are distributed across society. In terms of *political ecology*, there is a need to understand the power relations involved and how effective the catalysts that produce positive changes in behaviour and policy are likely to be, and how socially just management solutions can be designed and implemented.

We identify a number of priorities for natural and social scientists:

(i) more effectively communicate the evidence base that already exists so that scientific knowledge is communicated to decision makers and other stakeholders in constructive, useful ways that can generate political will as well as inform actions;
(ii) identify and address the key yet tractable knowledge gaps in ecosystem science. Many aspects of complex ecological systems will remain intractable for timescales longer than the timescales available to implement evidence-based solutions;
(iii) identify how key elements of the complexity that enhance resilience and adaptation can be supported and propagated;
(iv) identify where there are synergies and trade-offs. Interventions that maximize synergies between different ecosystem services are crucial for solutions which have any prospect of scalability; and
(v) implement and/or maintain long-term monitoring, which is the only way to fully understand trajectories in complex contexts and evaluate the success of management interventions.

Climate change is ongoing, and within the next few decades, societies and ecosystems will either be committed to a substantially warmer world or major actions will have been taken to limit warming. Ecosystems play a major role in both of these scenarios. Extensive and connected ecosystems, species and genetic diversity, trophic intactness and habitat heterogeneity, can buffer the impacts of climate change. NbS, such as ecosystem management and restoration, can play an important role in climate change mitigation and societal adaptation, but will only provide benefits if deployed in conjunction with a reduction in fossil fuel emissions.

At some point this century, as human civilization faces the decarbonization challenge, global atmospheric greenhouse gas concentrations are likely to stabilize, and global temperatures will peak. Judicious protection and restoration of ecosystems could have played a significant role in that stabilization, and could continue to play a role in the subsequent cool-down. The climate change that will already have occurred will inevitably have led to some ecosystem degradation and biodiversity loss. But in a world where NbS have been implemented at scale, ecosystems that are intact, extensive and connected have a much better chance of adapting and thriving in this new climate regime, and thereby of contributing to a vibrant and resilient biosphere that is needed for its own sake and for providing the fabric within which human societies exist and thrive.

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