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Biodiversity, climate change, and ecosystem services

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The capacity of ecosystems to deliver essential services to society is already under stress. The additional stresses imposed by climate change in the coming years will require extraordinary adaptation. We need to track the changing status of ecosystems, deepen our understanding of the biological underpinnings for ecosystem service delivery and develop new tools and techniques for maintaining and restoring resilient biological and social systems. We will be building on an ecosystem foundation that has been radically compromised during the past half century. Most rivers have been totally restructured, oceans have been severely altered and depleted, coral reefs are near the tipping point of disappearing as functional ecosystems, over half of the land surface is devoted to livestock and crop agriculture, with little consideration for the ecosystem services that are being lost as a consequence, some irrevocably so. We have already seen many regime shifts, or tipping points, due to human activity, even before the onset of measurable climate change impacts on ecosystems. Climate change, caused mainly by anthropogenic greenhouse gas emissions, will disrupt our ecosystem base in new ways. Already we are seeing widespread signs of change. Species behaviors are altering and disrupting mutualisms of long standing. We are seeing extinctions within vulnerable habitats and conditions where migrations are necessary for survival but where often there are no pathways available for successful movement in the fragmented world of today. These challenges represent an extraordinary threat to society and a call for urgent attention by the scientific community.

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The nature of the problem up to the present

The impact of humans on the biotic systems of the earth is dramatic and is accelerating. A global analysis of these changes revealed that over 60% of the services, or societal benefits, provided by biotic systems has been diminished through human activities, with the greatest loss occurring just during the past 50 years [1]. The extent of human modification of these biotic systems has been extraordinary, so much so that new maps of the earth are being drawn of the current boundaries, not of natural systems, but of the now predominating human-modified ecosystems [2]. These enormous impacts by plowing, grazing, fishing and hunting, timber removal, river diversions, city building, water extractions, polluting fertilizer additions and so forth are profound and in many cases growing in intensity. It is these activities that have disrupted ecosystem processes and diminished such a large fraction of ecosystem services. At the same time the benefits of enhancing the earth's systems to provide food, fuel and fiber for society have been remarkable and have supported burgeoning population growth. This achievement, however, has been at the expense of other services that benefit society. These tradeoffs have however not been analyzed to their full extent.

Climate warming is gaining momentum and is impacting upon these realities of the past. These changes will exacerbate many of the already existing adverse consequences of human activities on the sustainability of our biotic resources. In this article we describe the emerging climate change impacts on biotic resources and interactions. We look at these changes through the lens of ecosystem services since they represent an end point of a complex chain of players and interactions that are the providers of these services and further it is these services that are most relevant to society at large. We examine climate change impacts all along the chain, from species to ecosystem functioning, as well as looking at the impacts of past degradation along this chain due to longer term human drivers of change, in order to highlight the nature of the issues and consequences that society must confront in the near future.

Ecosystem service generation

In order to evaluate the impact to climate change on ecosystem services we take a reductionist view and examine how each of the biological and ecosystem components feed into services and hence human wellbeing. We examine how each has changed or will most probably change in the very near future.

In a given locality, organisms interact with the physical environment, and each other, as they compete for the building blocks for growth and reproduction, that is, water, nutrients and energy. These interactions in turn result in the mining of minerals from depths into living structures and back again to the surface, the movement of water from the soil through plants into the atmosphere, and the capture of carbon from the atmosphere, enabling the assembly of complex molecules and structures, and its subsequent release to the atmosphere through respiration and decomposition. These basic biogeochemical and growth processes represent the operation of an ecosystem. But there is more, the interaction and competition of the collected organisms result in a myriad of biochemical strategies for defense against predators as well as for structures and behaviors that promote the exchange of genetic material such as in pollination, often using intermediary species or collection of species for this task.

The end result of all of these processes and interactions is a functioning ecosystem that delivers services of benefit to society such as food, clean water, erosion control and cultural values. Further it can be demonstrated that the human activities described earlier can either enhance or destroy those interactions, that is, humans are interactive and a major component of these systems.

The ecological consequences of species and population losses

Not all species are equal in terms of how ecosystems function. Abundant and dominant species are generally the major controllers of system function, yet less abundant species may nonetheless have very consequential effects on ecosystems: such as ecosystem engineers and keystone species [3]. The presence of rare species may enhance invasion resistance in a community [4] and further, a given species may be rare at the present time, but change dramatically in abundance and importance at other times [5], supporting the idea of biodiversity as 'ecosystem insurance' [6].

Certain groups of species are by their very nature major players in any ecosystem; a case in point is the community structuring role of top carnivores. These are particularly susceptible to local, and global extinction, mostly due to human activities, particularly habitat loss [7], but also due to hunting. Because of their generally large home ranges these types of species are particularly susceptible to habitat fragmentation often resulting in the loss of an entire trophic level [8] with profound impacts ecosystem functioning. Meyers *et al.* [9] discussed a dramatic example of this documenting the consequences of declines in populations of great sharks in the coastal northwest Atlantic ecosystem. The decline resulted in increases in the population of rays, skates and small sharks. The increase in cownose ray was sufficient to reduce their scallop prey to a level that the fishery for them was terminated after a century of operation. Other examples of dramatic top–down control of ecosystem structure and process have been shown in marine systems [10] as well as freshwater and terrestrial systems [11].

Experiments have shown that the greater the diversity of functional groups in a system the less is the likelihood of cascading species extinctions [12]. If both functional diversity (how species control in an ecosystem processes) and response diversity (how species respond to stressors) within functional groups are high, an ecosystem may exhibit a great deal of resilience in the face of environmental changes [13]. A meta-analysis of work in eight different European grasslands suggests that different species have a disproportionate impact on different functions so that maintenance of multi-functional ecosystems may require maintenance of high species diversity [14].

The losses of the components of the ecosystem service delivery chain incurred to date

Species and populations

The documented losses at the species and population level are extensive and future trends from past drivers of change are continuing for the most part unabated. According to the IUCN Red List update in 2008 over 900 species have gone extinct since 1500 (http://www.iucnredlist.org/static/stats) including many vertebrates, invertebrates and plants. This is certainly an underestimate since our knowledge of many groups is extremely poor and further the time line for inclusion in the list can be lengthy.

We know most about the world's bird species. Since 1500 we have lost at least 150 species, and at present one in eight bird species are threatened with global extinction. Across 20 European countries 45% of the bird species have had population decreases [15]. In the grasslands of the United States 55% of the bird species are showing population declines and 48% are of conservation concern (http://www.stateofthebirds.org).

The picture for mammals is equally bleak. Estimates are that one-quarter of the over 5000 species of mammals are threatened with extinction (since 1500 76 species have gone extinct) and one-half of all of species have declining populations. For land mammals the principal driver of risk is habitat loss followed by harvesting. For marine mammals by-catch and pollution are the biggest threats [16].

Extinction rates of freshwater fauna are estimated to be at least five times higher than terrestrial or avian species [17] owing to the multiple stressors of overfishing, dam construction, water diversion and pollution.

System level losses

We are not only losing species and populations but we are also losing bits and pieces of entire communities and ecosystems and hence their ecosystem service delivery capacity. Understanding the extent of these losses sets the degraded baseline upon which climate change will be acting.

Terrestrial systems

The Millennium Ecosystem Assessment [1] reported that nearly three-quarters of the Mediterranean and temperate forests have been converted by human activities, and 5 other of the 13 biomes analyzed had undergone around 50% conversion. Only boreal forests and tundra, which are not suitable for agriculture, exist in a non-human-modified condition, although they are already show significant responses to climate change [18]. Projected rates of habitat modification suggest that over the coming decades conversion will be concentrated in tropical and semi-tropical forests and grasslands; areas that still harbor significant biodiversity and that are crucial for ecosystem services such as water regulation, and food and timber.

Marine systems

Marine ecosystems have suffered enormous losses over past generations [19]. The synergistic effects of habitat destruction, overfishing, introduced species, warming, acidification, toxins and massive runoff of nutrients are transforming once complex systems like coral reefs and kelp forests into monotonous level bottoms. 'Clear and productive coastal seas with complex food webs topped by big animals are being transformed into simplified, dominated by microorganisms, often ecosystems with boom and bust cycles of toxic dinoflagellate blooms, jelly fish, and disease' [20]. In Jackson's meta-analysis he notes that biomass (catch, cover) estimates of declines since pristine conditions indicate that in coastal seas and estuaries, over 80% of the most large-bodied vertebrates have been lost as well as 90% of the oysters, 65% of the seagrass, and 67% of the wetlands. Over the past 50 years we have fished deeper and deeper [21]. The environmental stressors on coastal systems are high and increasing as noted by the exponential increase in dead zones around the world that now amount to 245,000 km^2 of coastal marine systems [22]. The oligotrophic waters of the oceans that have expanded by 6.6 million km^2 in the past 20 years are most probably driven by global warming [23].

The principal ocean-derived ecosystem services used by humans including tourism, fisheries, nursery habitats are therefore all compromised [24]. Even benthic systems are important service players, providing food, bioactive molecules, nutrient regeneration and supply to the photic zone, and climate regulation. The functioning and provisions from these benthic systems is enhanced by species diversity [25].

Like their coastal counterparts, mangrove forests, coral reefs provide food and resources that largely underpin the survival of approximately 500 million people yet around 40% of coral reefs have been lost over the past 40 years, and losses continue at the rate of 1–2% per year [26]. This poses a grave threat to the millions of species that live in association with coral reef ecosystems [27].

Fresh water systems

Although fresh water systems, such as rivers, are biologically rich and play major roles in providing ecosystem services they have been one of the most altered ecosystem types on earth. Humans have optimized the capture of provisioning services of riparian systems—water, energy, transportation, and food, and given less attention to other ecosystem services such as carbon sequestration, temperature regulation, water purification, erosion and flood control and cultural services. Worldwide, over half of all wetlands have been altered. [28]. In the U.S. alone, 42% of the wadeable streams are impaired harboring very low biodiversity and more than half have had major changes in their high and low flows [29]. Agriculture is the source of 60% of all pollution in U.S. lakes and rivers; while in much of Europe municipal and industrial sources have contributed pollutant loads to lakes and rivers.

The degree of alteration of river systems by humans is illustrated by the fact that there are over 45,000 dams exceeding 15 m height that includes half of the large river systems of the world [30]. The flow regime changes induced by dams alters the ecological diversity and function of river systems as well as disrupting sediment flux and thermal regimes, among other important physical factors driving ecosystem functioning. The modification of flow regimes over such large parts of our rivers has resulted in biotic homogenization of the fish biota of the world, fostered by the introduction of fish species favored by the thermal and flow conditions induced by dams [31]. These large-scale river modifications by dams are just a part of the vast alteration of the watersheds of the world as humans capture water and other of the many resources that these systems provide including the fertile soils of the flood basins. Species losses have been drastic in many development schemes [32].

Climate change, biodiversity and the delivery of ecosystem service

Much of the damage described above has occurred over the past 50 years. It is upon this shredded natural world, with its impaired capacity to deliver of ecosystem services [1], which accelerating climate change will impinge. In the following we give some examples of the kinds of losses and impacts of climate warming that have already occurred and their consequences on ecosystem service delivery.

The future world

What do we envision in the world that is emerging as climate change grabs hold? The drivers of climate change, particularly changes in the composition of the atmosphere, such as increasing CO_2, affect organisms directly, as does the action of some of the other greenhouse gases, particularly nitrogenous compounds resulting from combustion and crop fertilization. The primary indirect effect of these drivers is climate warming itself that may have profound direct impacts on the metabolism of organisms. However, climate warming also has a range of indirect effects through changes in sea level and vegetation types that impact physical and biological systems. It is the combination of these direct and indirect impacts that are occurring at rates and extents unprecedented in recent times that make climate change such a complex but potentially hazardous force affecting ecosystems and their services.

Organisms will differ in their response to climate change. Some will cope better with changes than others as a result of their ecology and evolutionary history. But climate change is a different kind of threat from the major anthropogenic pressures of the past such as overexploitation and habitat change. In particular, its differential impacts on interacting species in a community may have widespread consequences affecting for example pollinator/plant and plant/herbivore relationships [33] as well as more complex features of ecological interaction webs [34]. Also, climate change will be rapid and may outstrip the potential for many organisms to be able to adapt and evolve [35] or to track suitable climates across the landscape. The possibilities will depend on the life cycle period of an organism as well as their basic genetic and phylogenetic characteristics. Not only will different lineages of organisms respond at different rates to climate change but also will habitat characteristics. For example, soil formation takes place over millennia through the interaction of climate and the biota, thus the rapid migration of organisms that will be stimulated by climate change will not only result in new combinations of species but also perhaps mismatches of the biota with the substrates upon which they evolved. Then there will be new climate combinations that have not been experienced by any of the extant biota [36].

The complexity of biotic response to climate change

As the climate continues to be altered we will see increasingly dramatic reconfigurations of the earth's ecosystems and their functioning, and hence their capacity to deliver ecosystem services. The impacts of global warming on biotic systems are already apparent as Parmesan [37] has noted: 'the direct impacts of anthropogenic climate change have been documented on every continent, in every ocean, and in most taxonomic groups'. Lenoir *et al.* [38] compared the elevational range shifts of 171 forest plant species growing from sea level to 2600 meters elevation in Western Europe and found an average upward range shift of 29 meters per decade. Shifts were not uniform however—herbaceous species with shorter life spans had greater distributional shifts than did woody species and species of higher elevations were more sensitive to warming than low elevation species. This then indicates a disruption of community structure with warming.

In a study of the distributional changes of mammals in Yosemite National Park over a 50-year period an average of 500 m upward change in distributional limits were found for half of the 28 species studied [39]. Lowland species increased their elevational distribution whereas high elevation species had their overall range contracted indicating again a restructuring of community relationships. Further, as Moritz *et al.* [39] noted, the kinds of range shifts they observed in Yosemite would not necessarily be observed elsewhere where potential corridors for migration had been severed by land use change, illustrating the interaction between land use change and climate warming in determining biotic outcomes.

These kinds of distributional shifts are not only restricted to temperate regions but are also being found in the tropics for both plants and insects [40,41]. Biota with good dispersal abilities and wide thermal tolerances may be able to shift their distributions. However, habitat loss, absence of migration corridors and/or for river ecosystems the absence of northern flowing waters in some regions may restrict movement of fish and prevent those that require prolonged periods of low temperatures from moving to colder regions [42].

The fraying fabric of species interactions

Climate change is not only altering the species' distributions but is also disrupting the web of interactions in communities including phenological shifts. Cleland *et al.* [43] noted that of 542 European plant species observed during the 30-year period from 1971 to 2000, on average, there was an advanced spring leaf unfolding by 2.5 days per decade and fruit ripening by 2.4 days per decade. Three-quarters of the species showed advances. Early season species showed the earliest acceleration and with some later season plants actually showing a delay. The complexity of the responses of plants that can be expected have been shown by an experimental study of Cleland *et al.* [44] where CO_2 enrichment, the major direct driver of climate change, accelerated flowering of forbs but delayed it in grass species.

Migration phenology of songbirds is also changing. Van Buskirk *et al.* [45] found that in a sample of 78 species over a 46-year period spring migration was significantly earlier but autumn migration was unchanged. As with plants, there was considerable variation among species particularly in the autumn migration period. A conclusion of this study was that these differences in species responses to migration would result in differences in community reassembly than has occurred in past times.

We are beginning to see the full consequences of these phenological shifts when viewed at the community level, for example, by examining the matches or mismatches in timing of members of trophic chains. Visser and Both [46] reviewed such cases and found that the phenology of a focal species shifted too early or too late in reference to their food sources ('the yardstick'). A particularly complex case has been found in marine systems where there are now extensive mismatches in production and supply among trophic levels and functional groups [47].

System responses to climate change

There are already indications of dramatic impacts of global warming at the system level, particularly in the arctic and for coral reef systems. Mass coral bleaching driven by warmer sea temperatures has killed vast numbers of corals across the tropics, causing some reefs to lose their ecosystem structure and functions [48]. Six major coral bleaching events have occurred across the world since 1979, when they first were reported in the scientific literature. These impacts are increasing and will become annual events by as early as 2030–2050 if sea temperatures continue to rise at current rates. Ocean acidification due to the increased entry of carbon dioxide from the atmosphere into the ocean, is adding further stress on reef building corals by driving down the concentration of carbonate ions that are crucial for coral calcification. Already, coral reefs on the Great Barrier Reef [49] and in Thailand [50] are calcifying 15% slower than they were in 1980. This reduction in calcification is unprecedented in the 400 years of coral record examined by [49]. There are large ecosystem service consequences to these changes. In the Coral Triangle (which spans six Southeast Asian countries) over 100 million people face declining food security and the exposure of their communities and towns to increasing sea level and storm intensity.

Extreme climatic events and ecosystems

In many parts of the world it is not the mean climatic conditions but rather the extremes that set the clock on changes in ecosystem structure and functioning. Unusually heavy rainfall and stormy periods as evidenced during El Niño events in California, for example, have been shown to alter ecosystem dynamics from the high mountains to coastal marine systems resetting successional clocks as well as entraining regimes shifts (grassland to shrublands) [51]. Jentsch and Beierkuhnlein [52] review the impacts of extreme meteorological events, such as cyclones, drought and heat waves, and heavy rainfall and flooding on ecosystem processes, all events that are predicted to become more frequent and are major system disruptors. They call for a new class of experiments that will examine the impacts of such events and to probe which systems may be most resilient to these perturbations [53].

Ecosystem feedbacks to the climate system: positive and negative

In the early global circulation models ecosystems were hardly considered. More and more features of the land and sea surface interaction with the atmosphere have subsequently been added [54] and have demonstrated the significant effects of ecosystem type and condition on local, regional and global climates and the consequences of ecosystem modification.

Feedbacks at the regional level often act to exacerbate the warming trend. In the arctic, effectively an early warning system for climate change impacts, we are already seeing changes in annual snow cover and the beginnings of vegetation changes that are influencing surface albedo with feedbacks to the climate system [55]. The albedo effects first demonstrated in the arctic [56] now appear to be operative in many other parts of the world as well, where darker surfaces are replaced by lighter surfaces, or vice versa [57]. In the arctic the melting point of permafrost is a key tipping point: the amount of soil carbon and methane generating capacity that is currently kept out of the climate system by frozen soils is extremely large. Adding to this positive feedback at high latitudes is the effects of increased wildfire [58].

The subtropical drylands are projected to become yet drier in a warmer world. Coupled with intensifying human use pressures, this is manifest as desertification, woodland degradation and deforestation—with consequences for biodiversity, carbon and dust emissions to the atmosphere and the wellbeing of the world's poorest people [59].

Land and ocean ecosystems are currently absorbing over half of the anthropogenic emissions of CO_2. It is known that the absorptive capacity of land ecosystems is saturating, and will turn to a source, perhaps this century. The oceans once seemed to offer an inexhaustible buffer to the global carbon cycle. It is now apparent that the rate of carbon uptake form the atmosphere, especially in the crucial Southern Ocean, is also slowing [60].

So what is the future?

In what follows we explore pathways for the maintenance of ecosystem services in face of climate change, starting by showing the evolutionary adaptive modes already being exhibited by certain groups of organisms. Then we discuss how society can adapt their practices to maintain service production in face of change.

Natural system ecological and evolutionary responses

Predictions about future distributions of species and populations to climate change are being made through the use of 'ecological niche' or 'climate envelope' models. This approach has provided stark estimates of what the ultimate outcomes may be for species losses. In a widely cited paper Thomas *et al.* [61] predicted on the basis of mid-range climate-warming scenarios for 2050 that 15–37% of species would be 'committed to extinction'. Commitment to extinction is of course not the same as predicting the equivalent number of extinctions within the same time period because the time period from loss of suitable habitat to eventual extinction may last from decades to centuries. Nevertheless this approach clearly indicates the potential severity of even moderate levels of climate change for species persistence, community structure and hence ecosystem function. A meta-analysis of many individual studies of different species and regions analyzed by [62] suggested 20–30% of plant and animal species would be at increasingly high risk of extinction as global mean temperatures exceed a warming of 2–3 °C above preindustrial levels. Their estimates are not substantially different from those of [63] though they included a much wider range of species, habitats and geographical areas.

The climate modelling approach has the advantage that on the basis of species occurrences alone it is possible to derive estimates of the impact of climate change, but there are important assumptions that may not be justified [64] and substantial differences among models that need to be taken into account [65]. Translating range changes into extinction risk also needs to be undertaken with reference to the species biology and ecology [66]. The most significant drawbacks of the approach are biological differences between species and communities that will determine whether species are climate-limited and able to cope with change, how rates of change will impact species persistence and any synergistic or antagonistic factors from other global change processes. In a detailed study of invertebrates [67] showed that temperate species have wider thermal tolerances than tropical species. The temperatures at which they now live tend to be below what would be optimal in terms of fitness. As a result, although temperature change is expected to be greater in the temperate areas than in the tropics, the change in fitness for tropical species is expected to be greater. In a spatially explicit modelling study of *Protea* [68] found that characteristics such as tolerance of suboptimal habitats and interactions with other environmental events such as fire frequency could have surprisingly big effects on persistence.

One important way in which populations will cope with climate change will be through evolutionary adaptation. Many assessors have assumed that evolution will be too slow but this is not necessarily the case. Under some circumstances evolutionary change can be very rapid [69] although this may be hard to sustain over long time periods especially for species with long generation times. In one recent example an annual plant, *Brassica rapa* exhibited very rapid microevolutionary change in response to a climate fluctuation that led to a multiyear drought [70]. There are likely to be important limits to the rates of climate warming that natural systems can adapt to and these should be deducible from both limits to evolutionary change and limits to the rates that species can move across the landscape tracking climate change. More work in this area will allow more reliable predications for climate change impacts on biological systems.

Societal responses

Climate change is not only altering ecological systems, biodiversity and ecosystem services, but poses also fundamental challenges for managers, policy-makers and other actors in developing strategies to respond to uncertainties in projected climate change impacts, and possible non-linear ecosystem responses [71].

Decisions will have to be made at the local level that deviates from long-term practices. For example, a decision facing farmers is how to deal with new phenological mismatches between forage grasses and the natural predators of insect herbivores; this might call for more insecticide use. Planting dates for annual spring planted crops will be crucial, but these depend on soil condition, and therefore winter and spring rainfall, whose future trends are uncertain.

At a more general level in relation to climate change and primary productivity [72] predict that by 2030 many food insecure regions will face even greater problems. Adapting to change will be complex and involve a large institutional and social challenge. Challinor *et al.* [73] have called for new modelling tools, combining socio-economic models with biophysical approaches, to understand and predict the crop productivity and social adaptive possibilities under various climate change scenarios.

Ecosystems with reduced resilience may still maintain function and generate services, but when subject to a sudden event (like an extreme flood or heavy rainfall), they may shift into another less desirable state [74]. This often involves passing a threshold into another stability domain, referred to as a regime shift. Regime shifts can produce large (and often unexpected) changes in ecosystem services, and these changes may be very difficult to reverse [75]. The perspective of a steady-state global equilibrium is gradually replaced by recognition of complex dynamic social–ecological systems [76] where changes may no longer be incremental but instead sudden and abrupt, making it very difficult to apply conventional economic instruments and measures of sustainability [77].

We believe that the climate-change crisis can be used proactively to stimulate innovation and learning within society to build resilience and produce forward-looking decisions and strategies that could contribute to a needed transformation of a social–ecological systems [74]. Specifically, future research on climate – ecosystem services – social systems should focus on (1) identifying different trajectories in adaptation processes in linked social–ecological system and (2) identifying how novel management of ecosystems may facilitate desirable transformations.

A call to action

It is clear that climate change acting upon the already severely impaired natural systems that support society calls for extraordinary new efforts and focus by the science community. We need to make progress on the science of biological diversity and the link between biodiversity and ecosystem services in order to reduce uncertainty in our predictions of the consequences of climate change. This will enable us to implement actions that will build resilience into the delivery of nature's services that are vital to societal survival. To accomplish this goal we need to:

a. Develop an integrated system for mapping the stocks and flows of ecosystem services, and their values, at multiple scales [78].
b. Strengthen our basic science program to bolster our understanding of the linkages among biological diversity, ecosystem functioning, ecosystem services and societal needs and adaptability.
c. Carry out bold new experiments, and model development that incorporate the full suite of global change drivers in order to prepare adaptation strategies for a variety of ecosystems, including our crops.
d. Develop conservation, restoration, and natural resource management plans that are proactive and based on maximizing ecosystem service delivery, considering tradeoffs among services, and that are resilient to projected global changes. These plans must take into account that we may not be able to manage to return natural ecosystems to previous states or conditions.
e. Focus more scientific attention toward adaptation in light of inevitable changes in ecosystem functioning and services in the coming years. At the same time we need to identify practices that, if modified, will mitigate the drivers of climate change.

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