

change: understanding and managing biodiversity and ecosystems

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Ecosystems around the world are already threatened by land-use and land-cover change, extraction of natural resources, biological disturbances, and pollution. These environmental stressors have been the primary source of ecosystem degradation to date, and climate change is now exacerbating some of their effects. Ecosystems already under stress are likely to have more rapid and acute reactions to climate change; it is therefore useful to understand how multiple stresses will interact, especially as the magnitude of climate change increases. Understanding these interactions could be critically important in the design of climate adaptation strategies, especially because actions taken by other sectors (eg energy, agriculture, transportation) to address climate change may create new ecosystem stresses.

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Ecosystems and biodiversity have long been threatened by natural and anthropogenic stressors (MA 2005; Mooney *et al.* 2009). A stressor is an activity or phenomenon that induces an adverse effect and therefore degrades the condition and viability of a natural system (EPA 2008). The stressors that have most damaged natural systems fall into four general categories: (1) land-use and land-cover change ([LULCC], including habitat

fragmentation and degradation, urbanization, and infrastructure development), (2) biological disruptions (introduction of non-native invasive species, diseases, and pests), (3) extractive activities (such as fishing, forestry, and water withdrawals), and (4) pollution (including chemicals, heavy metals, and nutrients). The combined impacts of these stressors are estimated to have altered more than 75% of Earth's ice-free land (Ellis and Ramankutty 2008) and virtually all reaches of the world's oceans (Halpern *et al.* 2008).

Climate change has emerged as a new and increasingly important threat to natural systems (Mooney *et al.* 2009). Climate change is a stressor in its own right, and it interacts with these other stressors in complex ways. Here we present a conceptual framework of climate interactions with other stressors, survey and categorize current knowledge about the intersection of climate change and these stressors, highlight potential interactions under future climate scenarios, and discuss the implications for developing effective response strategies.

■ Conceptual framework

Climate change affects biodiversity and ecosystems through a variety of pathways; because many ecosystems are already stressed, and because human adaptation and mitigation responses to climate change across sectors can also affect ecosystems, the effects are complex and interacting. The combined effects of climate change and other stressors typically result in increased stress on natural systems, although individual stresses can ameliorate each other. An activity that is a stressor in one system may have a different, neutral, or even positive effect on another system. These interactions can affect the timing, distribution, and severity of the stresses experienced by

In a nutshell:

- Climate change is projected to be an increasingly important source of stress for ecosystems, both directly and through complex interactions with other stressors
- Ecosystems that are already stressed due to habitat loss, extraction of natural resources, biological disturbances, and pollution are likely to be affected more quickly and severely by climate change
- Understanding the complex interactions between climate change and other stressors will be essential in designing effective strategies for adapting to climate change
- Climate adaptation and mitigation strategies may create new and sometimes unforeseen stresses on ecosystems, as well as introducing novel interactions with existing stresses

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ecosystems. In natural systems that are relatively undisturbed by human activities, climate change may increase susceptibility to additional environmental stresses. Human responses to climate change may further complicate these relationships, presenting additional and novel sources of stress.

Figure 1a highlights four pathways illustrating how a single climatic change and a single stressor can affect species, populations, or ecosystems. Figure 1b illustrates these pathways in the example of native salmon populations affected by the climatic stressor of temperature increases and the existing stressor of non-native salmonid encroachment. The pathways are as follows:

- (i) Climate change can directly affect species, populations, and ecosystems. In this example, climate-induced increases in stream temperature have a direct, negative impact on native salmon (Battin *et al.* 2007).
- (ii) Climate change can affect a pre-existing stressor and thus have an indirect impact on the species, populations, and ecosystems. For instance, projected increases in water temperatures may also favor non-native, more temperature-tolerant trout species (Wenger *et al.* 2011), thus indirectly increasing competitive pressures on native salmon.
- (iii) Climate mitigation or adaptation actions may directly affect the ecosystem. For example, farmers may respond to higher temperatures by increasing irrigation, thereby decreasing streamflow and degrading fish habitat.
- (iv) Climate mitigation or adaptation actions may indirectly affect the ecosystem. In this case, as increased irrigation depletes in-stream water, the remaining water will warm more rapidly, further favoring non-native salmonids.

Normally there will be multiple climatic changes and multiple additional environmental stressors, making it much more challenging to identify and categorize interaction pathways. Figure 2 illustrates more pathways for climate and other stressors to affect salmon in California's Central Valley. However, even this figure is not inclusive of all the possible interactions; for example, each environmental stressor can interact with any of the other stressors, and there may be interactions involving multiple stressors.

These pathways can be further organized by recognizing the different types of interactions among stressors. These interactions may be additive, such that the effect of multiple stressors equals the sum when each acts alone, or they may be nonlinear, so that the combined impacts have a different effect than the sum of the individual con-

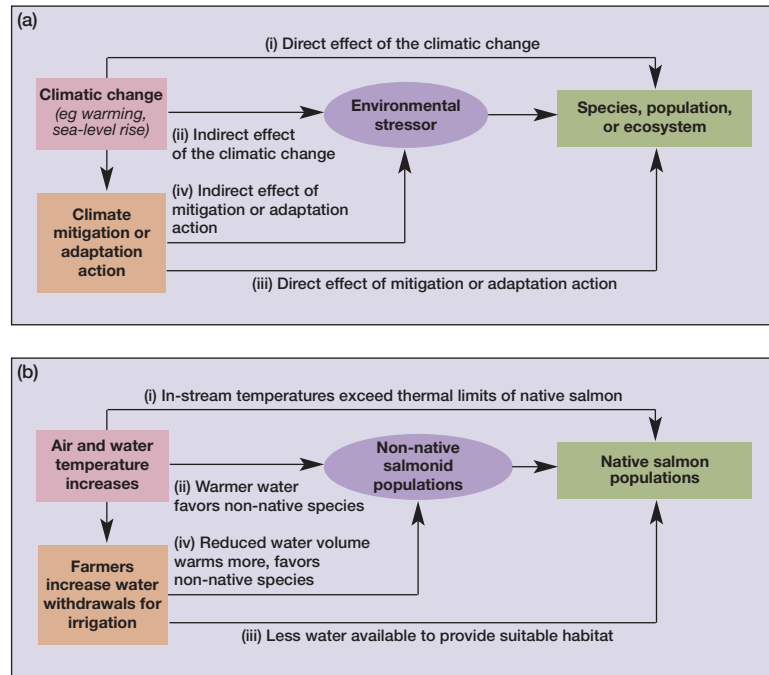


Figure 1. (a) General conceptual diagram of the pathways by which a single climatic change and another environmental stressor may affect a species, population, or ecosystem. A climatic change can (i) have a direct effect as a stressor in its own right, (ii) interact with another environmental stressor to either increase or decrease the effect of that stressor, (iii) induce a climate mitigation or adaptation response that has a direct effect, or (iv) induce a climate mitigation or adaptation response that interacts with another environmental stressor. (b) Application of the conceptual diagram to a specific example for native salmon populations. This example considers the combined effects and interactions between climate warming and the environmental stressor of non-native salmonids.

tributions (Brook *et al.* 2008). The existence of an additional stressor most often exacerbates the impact of a single stressor (ie is synergistic), although there are some cases in which a stressor can be antagonistic and will ameliorate the effects of other stressors (Folt *et al.* 1999). Most studies do not specify whether particular interactions are additive, synergistic, or antagonistic.

Climate change can also affect the character of a separate environmental stressor, specifically by affecting the timing, spatial extent, or intensity of the effects of that stressor. In California's Central Valley, for instance, increased incidence of drought may affect the timing of water withdrawals for irrigation, causing them to take place earlier in the season, for a longer duration, or with increased frequency (Figure 2; Fischer *et al.* 2007). In contrast, warmer stream temperatures are facilitating greater encroachment of non-native fishes, which threatens native frogs in the Sierra Nevada (Knapp *et al.* 2007); this is an example of an impact on the spatial extent of a stressor. If new climate conditions benefit an existing pest or invasive species, increasing the effects of competition or predation on native species, then this is a case of climate change affecting the intensity of a stressor.

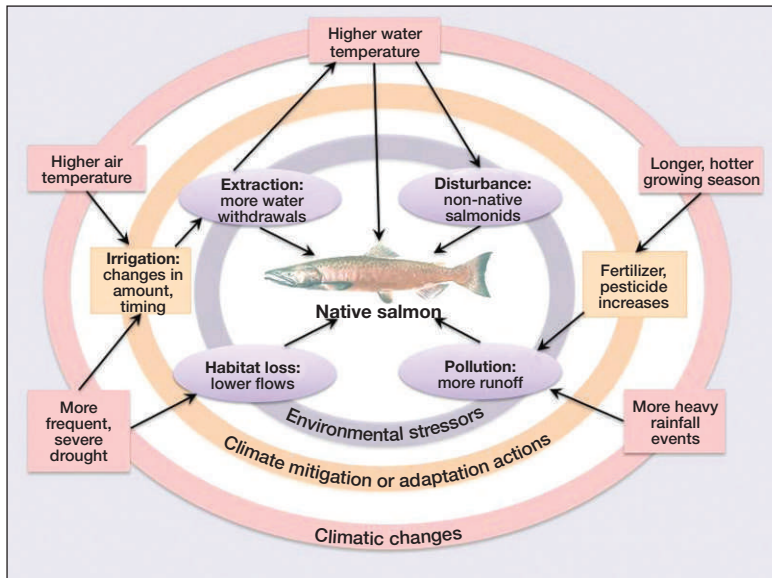


Figure 2. Conceptual diagram of the combined effects of and interactions among multiple climatic changes, climate adaptation actions, and other environmental stressors on native salmon in California's Central Valley. The colors correspond to those used in Figure 1.

■ Interactions of climate change with specific stressors

Climate change is already interacting with other environmental stressors to affect biodiversity and ecosystems. While the literature on the direct effects of climate change on species, populations, and ecosystems (pathway [i] in Figure 1a) has grown extensively in recent years (eg Grimm *et al.* 2013; Staudinger *et al.* 2013), less attention has been devoted to understanding and quantifying the interactions among climatic changes and other environmental stressors (pathway [ii] in Figure 1a). In this section, we summarize the current state of knowledge about these interactions, focusing on the four major categories of environmental stressors identified above: LULCC, extraction of natural resources, biological disturbances, and pollution. Figure 3 illustrates examples of species affected by the interaction of climate change with each of these categories of stressor.

Land-use and land-cover change

Widespread LULCC in the US has affected the amount, configuration, and quality of habitat and has altered hydrological and climatic regimes (Tilman *et al.* 2001). Habitat loss, degradation, and fragmentation are leading causes of terrestrial biodiversity loss, impairment of ecosystem functioning, and associated declines in ecosystem services (IPCC 2007; Krauss *et al.* 2010).

Climate change is likely to interact with LULCC in ways that further exacerbate these detrimental effects. For example, a recent meta-analysis of empirical studies found that biodiversity was more likely to be negatively affected by habitat loss in areas where precipitation rates

have changed (Mantyka-Pringle *et al.* 2012). One empirical study of butterflies in the Sierra Nevada of California showed that both habitat loss and climate change had likely contributed to declines in species richness (Forister *et al.* 2010). The rapid disappearance of the green salamander (*Aneides aeneus*) from the southern Appalachians of the US has been attributed to changes in temperature coupled with the salamander's limited ability to disperse in landscapes modified by logging, resort development, and dams (Corser 2001).

Only a few studies have explicitly projected future effects on species and ecosystems caused by the interactions between LULCC and climate change. Jetz *et al.* (2007) projected substantial range shifts for ~4.5–10% and ~10–20% of 8750 land bird species by 2050 and 2100, respectively; climate change was the primary driver of range contractions in temperate regions, whereas LULCC was the primary driver in the tropics. Similarly, the combined effects of LULCC and climate change are projected to bring about a loss of 7–24% of vascular plant diversity relative to 1995 by 2050, with climate change becoming a more important driver in the second half of this century (Van Vuuren *et al.* 2006).

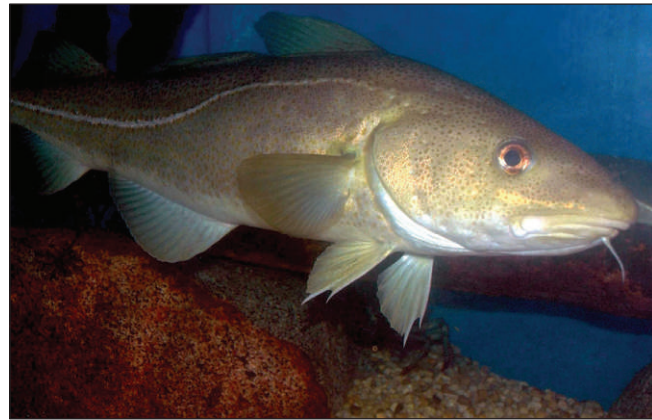
Land surfaces are major reservoirs of carbon (C), so LULCC could be a major driver of climate change if associated activities lead to more greenhouse-gas releases; alternatively, it could help mitigate future climate change if such activities help store or return C to the land surface (IPCC 2007). Actions such as clear-cutting or replanting major tracts of forests can also affect local weather patterns and the resulting potential capacity for biomass storage of C (Dale *et al.* 2011). As such, modifications to land use and land cover intended to address climate mitigation or climate adaptation may in turn interact with existing stressors or might directly affect species, populations, and ecosystems (via pathways [iii] and [iv] in Figure 1a).

Extraction of natural resources

Natural resources can be important ecosystem goods. However, their extraction can cause severe stress to species and ecosystems. Climate change can exacerbate these stresses, particularly if it further reduces the supply of a harvested resource. For example, a sufficient population growth rate in targeted fish species is one factor relevant to limiting fishery overexploitation. However, changes to the physical environment, such as water temperature, can affect individual growth, survival, and reproduction rates, and thereby rates of population replacement (Jonsson and Jonsson 2009). Likewise, water withdrawals combined with climate change are projected to have major effects on freshwater fish; for instance, Xenopoulos *et al.* (2005) projected that 25% of rivers



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Figure 3. Examples of species for which the interacting effects of climate change and other stressors have been documented. Green salamanders (*Aneides aeneus*, upper left) have declined in southern Appalachia due to the combination of warming and habitat fragmentation. Atlantic cod (*Gadus morhua*, upper right) in the North Sea, already severely depleted by overfishing, show poorer recruitment during warmer years. Eastern hemlocks (*Tsuga canadensis*, bottom left) are experiencing more attacks by the hemlock woolly adelgid, which is typically kept in check by cold winters. Adélie penguins (*Pygoscelis adeliae*, bottom right) are continuing to bioaccumulate dichlorodiphenyltrichloroethane (DDT), most likely due to its release by melting glaciers.

could lose more than 22% of fish species by 2070 due to the combined effects of increased water withdrawal and climate change. For three out of the four rivers examined in the US, the combined effects of climate change and water withdrawal were notably greater than the effect of climate change alone (Xenopoulos *et al.* 2005).

Resource extraction may also make ecosystems more vulnerable to climate change. The overharvesting of forests, for example, has the dual effect of causing local environmental damage that can decrease the resilience of an ecosystem to climate change and potentially compounding the magnitude of climate change itself by releasing stored C into the atmosphere (Hansen and Hoffman 2011). Furthermore, deforestation can lead to local warming and reductions in rainfall that can exacerbate climate impacts (Lawrence and Chase 2010). Despite the predominantly negative interactions between natural resource extraction and climate change, some interactions could have a positive impact or might make new resources available; for example, retraction of ice cover and earlier thaw in spring

may result in new fishing grounds in arctic regions. In some cases, forest harvest can result in localized cooling, counteracting climate-induced increases in air temperature (Gibbard *et al.* 2005). One study found higher levels of butterfly diversity adjacent to irrigated fields, suggesting that irrigation may mitigate the water-limitation effects of climate change in ecosystems adjacent to agricultural fields (González-Estébanez *et al.* 2011).

Biological disturbance

Biological disturbances include invasion by non-native species that have a competitive advantage, allowing them to spread rapidly; emergence of pest species that have expanded their range or are better able to survive milder winters; and disease outbreaks, whether novel, reoccurring, or introduced. Climate change will likely affect the severity, timing, and location of biological disturbances, as well as limiting the ability of the ecosystem to recover following such an event.

Climate change is expected to exacerbate the impacts of many introduced plant and animal species. Evidence suggests that some of these species have already responded to recent changes in the atmosphere and to climate (Walther *et al.* 2009), and future changes are likely to increase the ranges of several invasive plant species across the US (Bradley *et al.* 2010), potentially expanding their impact. In particular, changes in fire regimes will affect interactions among native and non-native species (Keith *et al.* 2008). Extreme climatic events that stress or kill native species are thought to temporarily increase communities' susceptibility to invasion (Diez *et al.* 2012); these events are projected to become more frequent with climate change. Although climatic changes may have strong effects on species ranges in the future, changes in the extent of different habitat types within a region have the potential to exert as much or more influence over the abundance of some invasive plant species (Ibáñez *et al.* 2009).

Climate change is also affecting the geographic ranges and virulence of many pests, pathogens, parasites, and disease vectors, and enhancing their ability to spread. For example, climate-induced habitat change has expanded the range of fungal pathogens that cause amphibian mortality (Pounds *et al.* 2006). The near-epidemic spread of pine and bark beetles in western US states (Bentz *et al.* 2010) and the northward expansion of the oyster diseases "MSX" and "dermo" to Nova Scotia (Ford and Smolowitz 2007) may also be linked to climate. On the basis of an assumption of a 2°C warming and changes in precipitation, Benning *et al.* (2002) found that extant Hawaiian honeycreepers may be driven to extinction through the combined effects of climate change, introduced avian malaria (spread by introduced mosquitoes), and historical land-use changes. As warming continues, hemlock woolly adelgids (*Adelges tsugae*), insect pests that have killed many eastern hemlocks (*Tsuga canadensis*) in recent years, are likely to expand their ranges northward (Dukes *et al.* 2009). Climate-change impacts on pests may have cascading effects: projected increases in temperature could increase the frequency and severity of insect outbreaks, and the resulting increase in tree mortality may in turn promote wildfires.

Forecasting changes in impacts from pests, pathogens, or invasive plant species is often fraught with uncertainties beyond those associated with forecasting climate change alone; often, too little is known about the climatic tolerances or responses of the species of concern to make confident projections under a given scenario (Dukes *et al.* 2009). Indeed, climate change may not always increase the net impact of introduced species, and some have argued it could be associated with the decline of pathogens, vectors, and hosts (Lafferty 2009). In areas that become climatically suitable for a new pest, pathogen, or host, other factors – such as competition, physical barriers, or predation – may still limit its range. Furthermore, climate change may reduce climatic suit-

ability for a species or induce other habitat changes that are less favorable to its spread (Slennig 2010).

Pollution

Climate change may magnify the adverse environmental effects of pollutants, including metals, pesticides, organic material, nutrients, endocrine disruptors, and atmospheric ozone (O₃; Hansen and Hoffman 2011). It also alters temperature, pH, dilution rates, salinity, and other environmental conditions that modify the availability of pollutants, the exposure and sensitivity of species to pollutants, and the transport patterns, uptake, and toxicity of pollutants (Noyes *et al.* 2009).

Climate change is affecting where and when pollutants are found in the environment. For example, changes in transport patterns, such as currents, wind, and river flows, may enable environmental pollutants to accumulate in new places, exposing biota to risk in different habitats. Some contaminants thought to be diminishing in concern, such as polychlorinated biphenyls, are being remobilized in the environment as a result of climate change. Persistent organic pollutants, deposited in glaciers during the period of heavy use in the mid-20th century, are now being released due to climate-induced ice melt (Blais *et al.* 2001). Adélie penguins (*Pygoscelis adeliae*) in western Antarctica, for example, have continued to bioaccumulate DDT over the past 30 years, most likely via DDT release from melting glaciers (Geisz *et al.* 2008). Altered pH can make heavy metals more biologically available in aquatic systems, thereby increasing their impact on the environment.

Climate change is also intensifying the effects of some pollutants. Rising temperatures, for instance, can enhance exposure to metals by increasing the respiration rates of fish (Ficke *et al.* 2007). Higher temperatures resulted in greater mortality rates in metal-exposed ectotherms in 80% of the cases examined, largely associated with increased biological uptake and accumulation of metals (Sokolova and Lannig 2008). Higher temperatures can also exacerbate hypoxic conditions because warmer water holds less dissolved oxygen than cooler water and accelerates the bacterial decay of organic matter, which in turn consumes more oxygen (Rabalais *et al.* 2009). More frequent extreme rainfall events can further exacerbate hypoxia by increasing the runoff of nitrogen and phosphorus (P) into waterways.

Finally, climate change may cause increases in some pollutants, most notably ground-level O₃. Many regions of the world are projected to have higher O₃ concentrations by the end of the 21st century (Sitch *et al.* 2007). Few studies have examined the potential consequences of O₃ pollution for biodiversity, and predictions are confounded by interactions across trophic levels. However, reductions in wild plant productivity as a result of O₃ exposure suggest that climate-induced enhancement of O₃ concentrations could affect biodiversity (Wittig *et al.* 2009). Furthermore, ground-level O₃ damage will likely offset some productivity gains in plants due to rising

Table 1. Examples of how climate change interacts with other ecosystem stressors and options for modifying conservation and management strategies to facilitate climate-change adaptation

Stress	Climate-change interaction example	Climate-change adaptation options
Habitat fragmentation and urban development	Many vernal pools in New Jersey coastal areas have been lost due to urbanization and development. Projected sea-level rise would fragment habitat by inundating the migratory routes used by eastern tiger salamander (<i>Ambystoma tigrinum</i>) and Cope's gray treefrog (<i>Hyla chrysoscelis</i>) (USFWS and NOAA 2012).	To create new corridors for amphibians, New Jersey is identifying areas to create new vernal pools at elevations above the projected sea-level rise and in places adjacent to existing protected lands (USFWS and NOAA 2012).
Fishery exploitation	The North Sea populations of Atlantic cod (<i>Gadus morhua</i>) have been severely depleted by over-harvesting. Cod species recruitment is weakened during warm years; thus, increasing temperature may compromise a full recovery (Olsen <i>et al.</i> 2011).	Fisheries management approaches such as harvest limits and temporary closures should factor in how short- and long-term climate changes affect recruitment rates.
Mining	Metal and acid pollution can accumulate in nearby topsoil during dry spells and then be washed into streams during heavy rains, posing a danger to aquatic life. Climate change is lengthening dry summers in the western US and bringing heavier rainfall, thereby increasing the risk of polluted runoff (Nordstrom 2009).	To be prepared for more extreme conditions, remediation efforts need to be designed to accommodate greater variability and shifting baseline conditions (Nordstrom 2009).
Invasive species	Cheatgrass (<i>Bromus tectorum</i>) is invasive in arid and semi-arid shrublands and grasslands of the Intermountain West, areas that are expected to become more arid with climate change. Cheatgrass also promotes fire, creating a positive feedback cycle favoring further invasion, the exclusion of native plants, and loss of carbon (Crowl <i>et al.</i> 2008).	Restoration efforts can be targeted in areas that are projected to become wetter and therefore less hospitable for cheatgrass (Bradley 2009).
Disease	Disease outbreaks in wildlife and humans caused by the bacteria <i>Vibrio</i> spp correspond with increased precipitation and rising ocean temperatures. <i>Vibrio</i> infections in the US have increased since 2000, corresponding to the frequency and severity of extremes in temperature and precipitation (Martinez-Urtaza <i>et al.</i> 2010).	Monitoring diseases in locations that are becoming climatically favorable, for example at the northern and upper elevation limits, can provide insight into where diseases are increasing in prevalence, inform efforts to control other stressors associated with disease spread (eg water pollution), and guide wildlife and public health interventions.
Nutrient loading and eutrophication	Parts of Lake Champlain have elevated P levels and have been experiencing dangerous and unsightly cyanobacteria blooms in recent summers (Facey <i>et al.</i> 2012). Runoff of excess fertilizer from agricultural fields is a major source of P pollution and could be exacerbated by climate-change-induced increases in heavy rainfall events.	The EPA is now working to update the 2002 P Total Maximum Daily Load for Lake Champlain to account for the implications of climate change, such as altered precipitation patterns and flow in the watershed (Zamudio 2011).

atmospheric carbon dioxide levels, thus reducing C storage on land and possibly contributing further to climate change (Sitch *et al.* 2007).

■ Implications for conservation, natural resource management, and research

Consideration of the multifaceted context in which biodiversity and ecosystems are being stressed will be critical for informing and prioritizing conservation strategies and natural resource management as climate change progresses. A failure to account for interactions may result in the implementation of climate adaptation strategies that are at best inefficient and at worst harmful. Fortunately, natural resource managers have considerable training and experience in addressing interacting environmental stressors; this institutional knowledge can be applied to climate adaptation strategies as well.

Reducing the impact of other stressors and increasing the connectivity of fragmented landscapes are already important components of most climate-change adaptation strategies (Stein *et al.* 2013). However, existing conservation actions to address non-climate stressors may no longer be sufficient to achieve desired outcomes (Hansen and Hoffman 2011), particularly if they do not address interactions among stressors and among potential response strategies. In many cases, available tools for responding to a particular stressor will need to be modified to incorporate the effects of climate change, as illustrated in Table 1. For example, there have been many suggestions regarding how to locate, design, and connect terrestrial reserves to accommodate new climatic conditions (Lawler 2009). Likewise, the regulations or policies that limit plant and animal harvest rates will probably need to be adjusted to reflect changes in distribution and abundance resulting from changing climates. In other

cases, new management approaches might be required. For instance, past practices that typically allowed pine beetle (*Dendroctonus* spp) infestations to run their course have proven ineffective in recent years; the beetle propagated unchecked when the cold-weather conditions that typically regulate outbreaks failed to occur (Bentz *et al.* 2010).

The potential for maladaptive management strategies that address one stressor but exacerbate another is an additional factor in the effective stewardship of biodiversity and ecosystems in the context of climate change. As portrayed in our conceptual framework (Figures 1 and 2), climate adaptation strategies – for the benefit of either human or natural systems – can become new stressors themselves. Many of the tools used to control pests and disease outbreaks (eg pesticides), for instance, can have other adverse effects that may be compounded by climate change. Research is still needed to clarify how best to identify possible unintended consequences and reconcile different objectives.

A better understanding of the interactions between climate change and multiple environmental stressors will be essential for developing management strategies. There is only a nascent understanding regarding the precise pathways, types, and character of interactions. Yet, combinations of stressors will shape the ecosystems of the future. In particular, the presence of multiple interacting stressors increases the likelihood of broaching thresholds or tipping points that cause a system to rapidly shift to a new state. Future research should prioritize the development of analytical frameworks and tools to screen ecosystems for vulnerability, to model and identify critical thresholds, and to study interactions among climate and other stressors explicitly.

A critical barrier to investigating how multiple stressors interact is the lack of national networks that combine climate, biological, and stressor information, including explicit data on population structure and abundance for invasive, rare, imperiled, and other key species. Such networks would allow researchers to combine information on projected climate changes with species biological data to understand possible future range shifts, to consider how other environmental stressors would influence future species distributions, and to better attribute different impacts to climate change or other stressors. This more detailed understanding will be essential for developing effective natural resource management strategies that will mitigate the effects of a changing climate.

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