REVIEW

Getting ahead of climate change for ecological adaptation and resilience

Jonathan W. Moore[1]* and Daniel E. Schindler[2]*

Changing the course of Earth's climate is increasingly urgent, but there is also a concurrent need for proactive stewardship of the adaptive capacity of the rapidly changing biosphere. Adaptation ultimately underpins the resilience of Earth's complex systems; species, communities, and ecosystems shift and evolve over time. Yet oncoming changes will seriously challenge current natural resource management and conservation efforts. We review forward-looking conservation approaches to enable adaptation and resilience. Key opportunities include expanding beyond preservationist approaches by including those that enable and facilitate ecological change. Conservation should not just focus on climate change losers but also on proactive management of emerging opportunities. Local efforts to conserve biodiversity and generate habitat complexity will also help to maintain a diversity of future options for an unpredictable future.

The need to rectify human impacts on Earth's climate system is of dire importance, yet there is a parallel urgent need to implement conservation strategies that will enable adaptation of species, promote ecosystem resilience, and maintain the coupled human-ecological systems that support humanity. Even the most aggressive emission reduction strategies will mean that further warming will persist for decades before recovering; it is likely that that warming will exceed 1.5°C for multiple decades, even under very low greenhouse gas (GHG) emissions (*1*). Robust policies and approaches are needed that will provide the best opportunities for promoting ecological adaptation and resilience in a climate-challenged future. Here, we provide an overview of expectations and approaches for maintaining a functioning biosphere that may require thinking outside the box that is typically operated within for managing natural resources and conserving biodiversity.

Ecosystems and society are complex and dynamic systems with connected processes that interact across a hierarchy of scales that can produce resilience—the ability of a system to maintain key functions when disturbed (*2*). System resilience will arise from differential responses, shifts, and turnover in system composition, whether they are genes, populations, species, or habitat conditions. Thus, management for fluidity and connectivity and the expression of heterogeneity within systems can enable resilience (*3*). By contrast, exposure of systems with lower resilience to stressors may push them to undesirable states or compromise their aggregate ecosystem functions, including services to humanity. In the context of climate change, we use the term "adaptation" in a broad sense to refer to these evolutionary, ecological, and social changes that reduce the vulnerability of systems to disturbance (*1*).

> **"...conservation efforts will need to embrace the dynamic aspects of the biosphere..."**

Shift happens

The biosphere is fluid (*2*): Organisms adapt to changing environmental conditions; respond to their predators, competitors, and diseases; move into new habitats; and disappear from places that become inhospitable. These kinds of changes have occurred over the history of the biosphere, including the past 100,000 years (Fig. 1). During the last glacial maximum, 25,000 to 19,000 years ago, the ocean was ~120 m lower, and the world was 10°C colder than it is currently. Ice covered 25% of the terrestrial landscape, and low precipitation and temperatures limited forest cover. As the climate warmed, glaciers melted, and sea level rose rapidly, inundating coasts. Although these global transformations might seem incomprehensible, most species we see today coped with them [for example, most extant vertebrates evolved more than a million years ago (*4*)].

Anthropogenic climate change is driving a new era of rapid change in Earth's climate. The world has already warmed by 1.1°C, and sea level has risen by ~20 cm over the past century (*1*). These changes are small in magnitude relative to historic changes, but there are several critical differences. First, the pace of contemporary change is unusually fast. Second, Earth is predicted to warm to temperatures that have not occurred for more than 100,000 years (*1*). Third, humanity is simultaneously inflicting myriad other stressors that reduce the complexity, fluidity, and resilience of the biosphere. Human-caused extinctions are 100 to 1000 times higher than background rates (*5*), and 38% of terrestrial forest has been converted for human use (*6*). Fourth, humanity has developed infrastructure, governance, cultures, resource management systems, and ethics with only superficial consideration of the oncoming rapid changes to the biosphere that will occur in the near term (*7*).

The biosphere has repeatedly demonstrated its fluidity across scales of biological organization, ranging from the genes within a species to socioecological systems. Intraspecific genetic variation can change across space and time, driven by a dynamic adaptive landscape. For example, contemporary environmental variation and climate extremes, as well as occasional hybridization events, drove rapid evolution in the beaks of Darwin's finches for them to shrink then expand and then shrink again

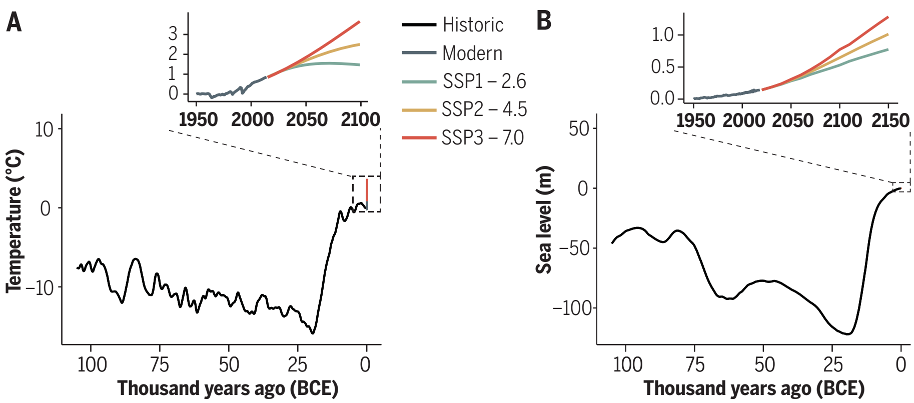

Fig. 1. A dynamic climate, from 100,000 years before present to 2100. Data are anomalies from the present conditions. (**A**) Historically reconstructed surface air temperature (*51*). (Inset) Modern surface air temperature records and projections under three emission scenarios (*1*). (**B**) Reconstructed sea level (*51*). (Inset) Modern sea level records and projections to 2100 (*1*). The projected climates are based on Intergovernmental Panel on Climate Change (IPCC) future GHG emission scenario SSP1-26 (teal), SSP2-45 (yellow), and SSP3-70 (red), representing low, intermediate, and high future emissions, respectively.

[1]Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada. [2]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA.
*Corresponding author. Email: jwmoore@sfu.ca (J.W.M.); deschind@uw.edu (D.E.S.)

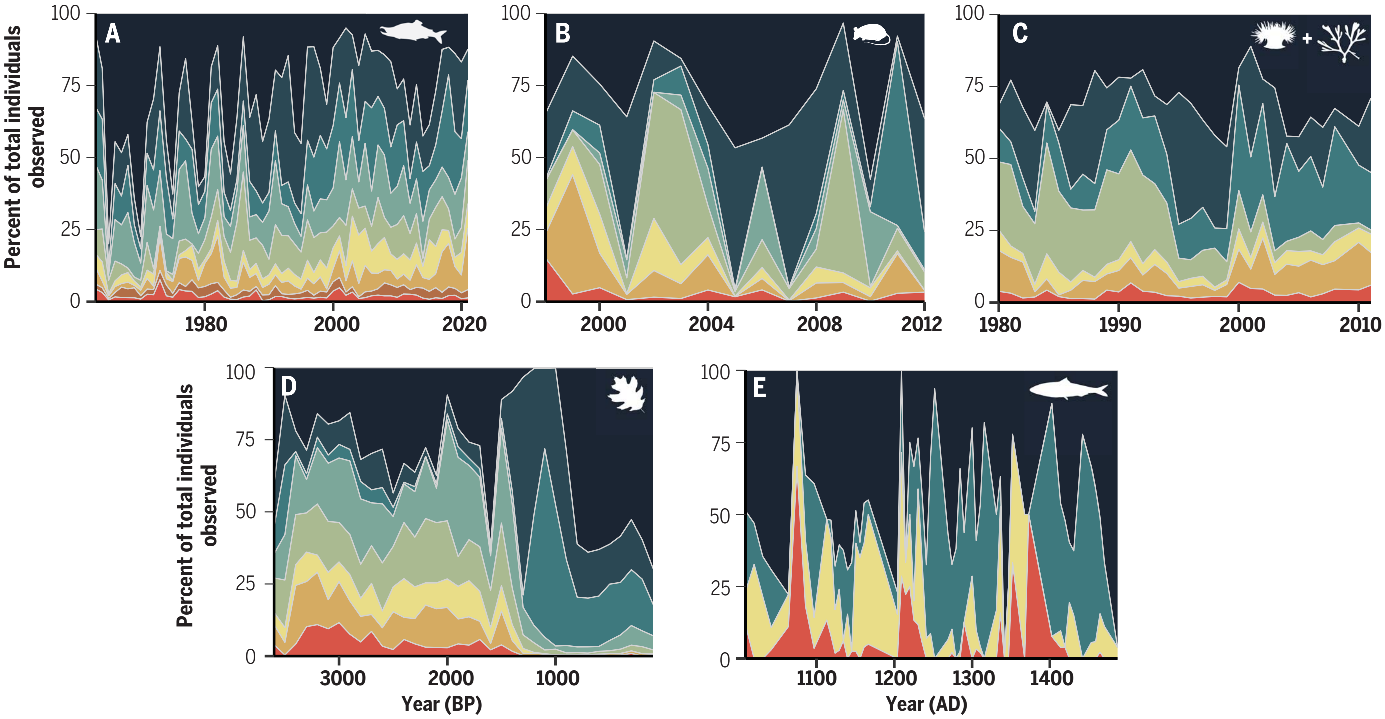

Fig. 2. Shifting biodiversity and turnover within ecosystems. (**A**) Sockeye salmon adult populations returning to nine major rivers in Bristol Bay, Alaska, USA. Data are updated from the Alaska Department of Fish and Game. (**B**) Rodents and marsupials captured in the Atlantic forests of South America (*52*). These data are presented from top (darker cooler color) to bottom (warmest color): *Akodon*, *Oligoryzomys*, *Euryoryzomys*, *Delomys*, *Didelphis*, *Marmosops*, *Marmosa*, and *Nectomys*. (**C**) Kelp forest community structure at San Nicolas Island, CA (*53*). These data include kelp and algae, and invertebrate species: *Cystoseira osmundacea*, *Dictyota binghamiae*, *Diopatra ornata*, *Corallina officinalis*, *Balanophyllia elegans*, *Cucumeria fisheri*, and *Corynactis californica*. (**D**) Fossil pollen counts from Siberia (*54*) for most abundant tree genera: *Pinus*, *Betula*, *Alnus*, *Poaceae*, *Caryophyllaceae*, *Artemisia*, and *Primulaceae*. (**E**) Relative abundance of marine fishes from Santa Barbara basin based on fossil scale counts (*46*): Northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*), Pacific sardine (*Sardinops sagax*), and Surf perch (*Embiotocidae* spp).

over 30 years (*8*). More generally, driven by both genetic change and plastic life histories, the phenologies of species are shifting in response to contemporary climate and environmental change (*9*).

Species' distributions and range boundaries also continuously change through time. For example, over the past 20,000 years, rapid climate change during glacier retreat drove interlinked processes of adaptation and migration in tree species (*10*, *11*). Pollen records reveal that trees spread poleward rapidly after glacier retreat, aided by small-scale refugia and local adaptations (*10*, *11*).

Contemporary climate change is also redistributing biodiversity, pushing species deeper in oceans, up mountains, and toward the poles (*12*). Terrestrial and marine species are moving poleward an average of 17 and 72 km per decade, respectively (*12*). However, if species' ranges follow shifting thermal regimes, they will not just head poleward given topographic complexities such as mountains, valleys, and coastlines (*13*). Instead, the direction and pace of climate change is extremely variable across the world. There may be climate sinks, such as the tops of mountains or coastal peninsulas, where species are pushed into local dead ends. Alternatively, some areas will be refugia, where environmental conditions remain hospitable. Thus, even simple thermal niche models highlight the complex forcing of climate warming on biological systems across a heterogeneous world.

Ecological communities within a given location also shift unpredictably with climate change as species flourish, wither, or invade (Fig. 2). Pollen records indicate that a plant community in Siberia shifted around 1500 years ago from birch and pine trees to be dominated by herbaceous flowering plants, such as primrose (Fig. 2). On more contemporary time scales, kelp forest communities over 30 years oscillated across years and decades from being primarily brown algae to predominantly cup corals and sea anemones (Fig. 2). Approximately 120,000 years ago, the pelagic fish community in the Humboldt Current off the coast of western South America was composed of small-bodied goby-like fishes when waters were warmer and lower in dissolved oxygen, whereas currently this community is dominated by anchovies that compose upward of 15% of the global annual fish catch (*14*). Analogous dynamics are expressed within metapopulations—for example, the productivity of different salmon populations shift asynchronously over time (Fig. 2). From trees to fishes, biological systems are not characterized by a single static equilibrium state but instead by turnover and compositional shifts across a range of time, space, and taxonomic scales (Fig. 2).

Community changes that involve habitat-forming species, ranging from kelps to corals to trees, alter the fundamental structure of ecosystems. The majority of vegetation communities have gone through large compositional and structural changes over the past 20,000 years (*15*). Contemporary global change is also driving ecosystem transformations, including the production of no-analog ecosystems where new assemblages are emerging with species extinction, invasions, and altered environmental conditions, such as in the transformation of Australian *Eucalyptus* forests to non-native annual grasslands (*16*).

The past 10,000 years of relative climate stability and favorable warm and moist climate conditions led to the emergence of agriculture and modern humanity. Yet even over this period of relative climate stability, people tracked shifting resources over vast distances, diverse cultures and practices adapted to shifting food sources, or in some cases, societies collapsed during extreme climate events (*1*, *17*). At times during humanity's history, colonization of people to new regions led to overexploitation of species and extirpation (*5*). Human activities have also shaped the biosphere such as by landscape burning, cultivation, and building structures (*17*). Humanity is now in a global crisis of its own making, with human-caused climate change causing risks and harm distributed unevenly around the world.

Forward-looking conservation and management

Natural resource management and conservation efforts will need to embrace the dynamic aspects of the biosphere to help maintain functioning ecosystems and protect biodiversity given oncoming climate change. In Holling and Meffe's visionary 1996 paper (*18*), they described a pathology in natural resource management in which desire to make ecosystems more predictable has led to the development of policies that seek to reduce natural variation in ecological systems. Paradoxically, such approaches can reduce ecosystem resilience to new change that lead to surprises that management agencies are not able to cope with, such as policies of fire suppression leading to catastrophic fires. Here, we adopt their view that "[e]cosystems are moving targets, with multiple potential futures that are uncertain and unpredictable" and emphasize that maintaining the fluid and complex nature of ecosystems is of ever-increasing importance for conservation and resource management (*18*). First, this paradigm would encourage compositional turnover in ecosystems, range shifts, and microevolution in species and flexibility in the human components of ecosystems (Fig. 3). Second, there is concurrent need to also conserve heterogeneity and biodiversity, from genes to species to habitats within ecosystems, that represent evolutionary and ecological options for a changing world, as well as the processes that generate this heterogeneity (Fig. 3). Although there has been extensive attention focused on specific interventions for adaptation to climate change, ranging from assisted gene flow to genome-editing technology such as CRISPR, here instead we focus on approaches to enable the intrinsic resilience of species and places as key components of complex socio-ecological systems during this era of rapid ongoing change.

Species can adapt rapidly to climate change, either through evolutionary adaptation of traits that reduce sensitivity to climate effects, such as physiological thermal tolerance, or decrease their exposure to climate effects, such as by shifting their phenology of key life-history events and geographic ranges (*19*). Oncoming range shifts mandate that conservation science and management grapple with defining what are native, non-native, and invasive species (*20*). Human activities have directly and indirectly increased the movement of many taxa, leading to widespread introduction of species, especially beyond major biogeographic barriers, and corresponding extinctions of native species as well as biotic homogenization. However, species movement into new habitats has always been key to the biosphere's adaptive response to a changing world, and protectionist perspectives could hinder community adaptation (*20*). Perhaps if species are following their projected climate trajectory, then they should be considered "proactively native."

Predicting range shifts by using bioclimatic models to inform spatial conservation efforts are now common. Forward-looking spatial planning for conservation could prioritize refugia, future habitat, corridors for connectivity, and maintenance of landscape heterogeneity. Yet the fine-scale impacts of climate change on species distributions remain highly uncertain because models are used to predict complex systems into no-analog climates (*21*). For example, a study of distributions of European birds found that observed changes varied markedly from predictions for 90% of studied species (*21*). Risk-dispersion approaches are more likely to capture locations that allow species to persist in the future and to include habitats that are underappreciated as critical for certain life stages of target species (*22*). Individuals from populations in nonrefuge areas may provide the genetic material needed for adaptation in the future that could be lost by narrowly focusing on protection of climate refugia alone (*23*). For example, corals from hot regions contain the genes for thermal tolerance that, with sufficient time and connectivity, could enable successful adaption of coral reef systems to warmer waters (*23*). Thus, we caution against the use of overly prescriptive approaches for identifying climate refugia and prioritizing these sites for protection at the expense of maintaining heterogeneity and a range of options across landscapes at local to regional scales.

Most natural resource management is tied explicitly to specific geographic locations. It has also been argued that people's connection to a "sense of place" strengthens such place-based strategies for managing and conserving resources (*24*). However, the composition and identity of places will shift as climate impacts are expressed locally and across the broader landscape. Specific species and ecological communities that are deeply foundational

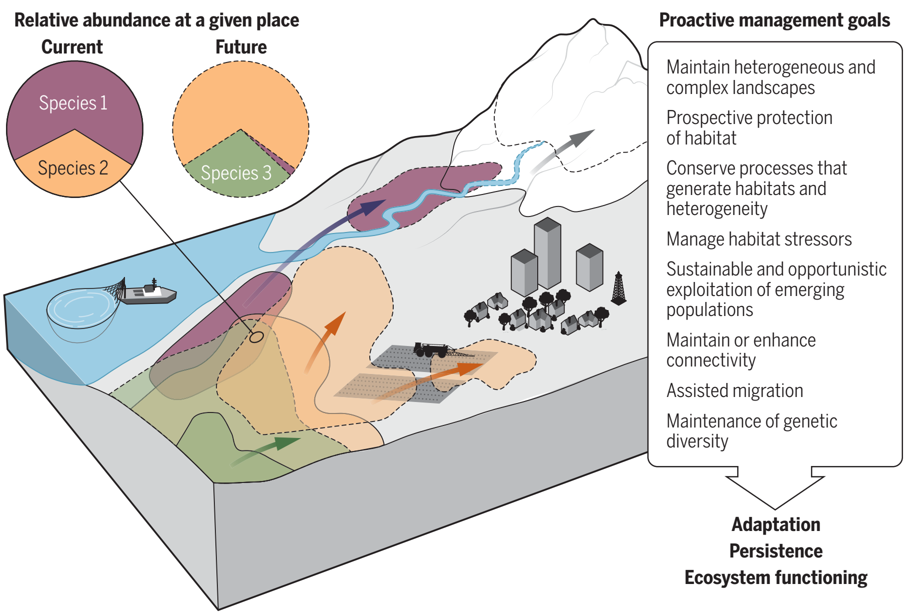

Fig. 3. Expected ecological changes and proactive conservation approaches for enabling adaptation in a rapidly changing world, from genes to ecosystems. Changing climate will transform ecosystems, such as through shifts in snow and ice cover (white region), and also cause changes in the species composition of future ecosystems, including loss of some species and additions of others. Pie charts indicate predicted community composition for current (solid-line chart) and future (dashed-line chart) community composition for a specific location (oval). Ecosystem-based management should enable flexible adaptation of human activities that depend on exploitation of species in specific locations, and the composition of existing protected areas are likely to look fundamentally different from when they were established. Species ranges will change, likely moving poleward and up in elevation as organisms track shifting suitable habitat (solid outlines indicate current ranges, and dashed lines indicate predicted ranges). Maintaining the processes and disturbances that maintain habitat heterogeneity will likely facilitate movement across landscapes and provide options for suitable climate in a climate-altered future.

ILLUSTRATION: KELLIE HOLOSKI/*SCIENCE*

to the identity of places and values of people are already starting to disappear, challenging cultural identities and values (*25*). Place-based management will likely continue to be the norm in most terrestrial and nearshore marine ecosystems, these local management systems will be confronted by unforeseen dynamics that may test their willingness and ability to adapt (*2*).

Reducing cumulative impacts of local stressors can offset the impacts of climate change in some situations. For example, thermally sensitive freshwater fishes are threatened by warming water temperatures in some regions. However, river water temperatures are not just affected by climate but also by removal of riparian forests, an extensive impact in many watersheds attributable to logging, agriculture, or urbanization. One study of a river in western North America estimated that intact riparian forests can reduce maximum summer water temperatures by 7°C, offsetting even a 4°C increase in future air temperatures by 2080 (*26*). Similarly, the combined impacts of climate warming and nonpoint nutrient pollution are increasing the eutrophication of coastal and inland waters and associated hypoxia, toxic algae blooms, and fish kills (*27*). Thus, cumulative stressors can exacerbate many impacts of climate change. Reciprocally, there is enormous opportunity for local habitat protection and restoration to offset or reduce the local consequences of climate change (*16*, *28*).

A primary goal for conservation policy to maintain resilience to global change is to conserve heterogeneity within ecosystems and their biota (*28*). Habitat heterogeneity is expressed across a range of spatial and temporal scales and is produced through a diverse assortment of biotic and abiotic processes. Restoration and maintenance of this heterogeneity has traditionally focused on the features of habitat themselves, rather than on the processes that generate them in the first place (*18*). Emerging restoration paradigms emphasize the latter—that conserving the processes that generate habitat heterogeneity is more likely to produce the features important for ecosystem resilience and species persistence (*29*). Long-term efforts to suppress and control disturbances have likely eroded the resilience of ecosystems and their ability to adapt to the new conditions that lay ahead with climate change and further growth of humanity (*18*). Protection of complex landscapes as dynamic habitat mosaics will enable their composition to turn over and maintain function. For example, salmon fisheries in Alaska rivers are stabilized within heterogeneous watersheds because of the complementary dynamics among tributary populations as they respond differentially to local-scale expressions of regional climate forcing (*30*).

A primary approach in conservation has been to establish permanent protected areas that are intended to shield habitats and species from cumulative human pressures. However, many species may move away from static protected areas, and the composition of protected habitats will turn over as climate imposes new conditions on the landscape (*31*). Thus, there is a need to expect that this approach may fail to conserve the habitats and species that originally motivated the formation of protected areas and that new collections of species may emerge (*31*). Recent emphasis on networks of protected areas with ecological connectivity among individual sites will enable the dispersal needed for species adaptation and persistence and potential for community turnover needed for broad-scale adaptation to new climate conditions (*22*, *23*, *32*). Beyond protected areas, the effective management of "working lands" as ever-evolving socioecological systems will also be a key component for proactive maintenance of ecosystem services, connectivity, and local biodiversity at landscape scales (*16*, *33*).

Dynamic management approaches have recently emerged to more effectively protect species in a state of flux. In such dynamic management approaches, spatial data on environmental conditions, animal movements, and the distribution of resource users (such as fishers) are integrated to adaptively shift protected areas to achieve conservation goals but also allow other sectors to use the resource. In marine ecosystems, dynamic ocean management has become an increasingly popular idea for protecting mobile species while enabling resource extraction activities that do not cause long-term ecological damage (*34*). The principal strategy is to provide moving spatial protection to mobile vulnerable species by continuously updating where they are susceptible to human activities, such as by-catch in fisheries for more common target species. Such dynamic approaches in ocean conservation offer promise but may be challenged by limited enforcement; cross-jurisdictional movements of species (*35*); and the need for coordinated and intensive monitoring, assessment, and forecasting of the status and distribution of vulnerable and targeted species. Dynamic management approaches also hold promise in some terrestrial systems, such as renting wetlands from farmers during specific seasons for migratory waterbirds (*36*). However, human impacts to landscapes can be long lasting, and thus dynamic approaches in terrestrial systems may be more spatially limited or responsive over longer time scales (*37*).

Management can also protect or restore habitats that are important future options for species. Human activities often eliminate viable future options for species, whether through invasive species, migration barriers, or habitat degradation. For example, coastal development often blocks the upslope migration of coastal wetlands in response to sea-level rise (*38*). Amphibians use both montane wetlands and lakes for breeding habitats. Yet even as climate change increasingly dries up wetlands, the more climate-resilient lakes have largely been removed as viable options for amphibians by the systematic introduction of predatory non-native trout to historically fishless lakes (*39*). Forward-looking protection or restoration actions can provide the future habitats that species might need to survive in a climate-altered future.

Oncoming ecosystem transformations from climate change are creating opportunities for some species but also frontiers for extractive industries, calling for preemptive habitat protection of nascent ecosystems. Ice retreat, whether it is in the polar oceans or glaciers, is

Box 1. Ecosystem transformation of the Arctic Ocean.

In the Arctic, what used to be covered in ice throughout the year is now increasingly open water during the summer. Minimum sea ice extent decreased by 30% over the past 29 years (*1*). Some species are threatened by ice retreat, with polar bears being the poster-child climate-change loser. Ice retreat is altering oceanic processes in complex ways that are difficult to predict; for example, the retreat of ice in the northern Bering Sea has changed food webs such as through reductions in ice-reliant and lipid-rich algae. Yet general predictions are for many fish stocks to shift poleward and for a >75% increase in biomass by 2100 in some Arctic marine regions (*40*).

The Arctic transformation to ice-free summers is bringing human industrial pressures. With the potential of increased fish stocks and increased access, there is promise of emerging fisheries. New shipping corridors are also opening up, driving rapid increases in shipping traffic and associated environmental risks, such as ship strikes to marine mammals (*55*). The continental shelf in the Arctic Ocean is also thought to contain substantial fossil fuel reserves—31% of unexplored natural gas and 13% of oil.

There are emerging efforts for forward-looking and precautionary governance of this rapidly transforming Arctic and its oncoming pressures. Canada and the United States have a temporary moratorium on Arctic offshore oil and gas licensing. Recent international fishing agreements emphasize precaution (*56*). Yet governance of this climate frontier remains complex and fraught among the five bordering states and other interested parties.

creating new ecosystems. For example, the Arctic Ocean is rapidly transitioning to having ice-free summers. Although this transformation is threatening ice-dependent species, ranging from polar bears to diatoms, major increases in Arctic fish production are expected over the next century (*40*), creating opportunities for fisheries. However, ice-free summers are also increasing Arctic shipping traffic as well as oil and gas exploration, which pose major environmental risks. Emerging initiatives are working toward forward-looking management of this multijurisdictional and contested resource frontier (Box 1). Alpine Glacier retreat is raising similar challenges. Glacier loss threatens water supply for hundreds of millions of people, as well as ecological flows and temperatures in downstream aquatic ecosystems (*1*). Yet in some local regions in western North America, glacier retreat is exposing new habitats, such as for migratory Pacific salmon that support fisheries. In the next 80 years under a moderate climate scenario, glacier retreat is predicted to create ~6000 km of new streams accessible for Pacific salmon and other stream-associated species (*41*). However, mineral development is targeting the retreating edges of icefields to mine newly exposed deposits (*42*). Thus, although climate change is creating local opportunities and options for species, extractive industries that can cause long-lasting environmental damage could preemptively undermine these options. Proactive protection of these frontier habitats would enable the realization of these future opportunities for species and associated sustainable use.

Industries and communities dependent on natural resources could more effectively realize the benefits of taxonomic turnover for stabilizing ecosystem services. For example, fishing communities are more resilient to climate perturbations when fisheries are allowed to harvest new species to replace those that become locally extirpated because of climate fluctuations (*43*, *44*). Flexibility in what fishers can capture provides for stability, particularly given the tendency of fish populations to boom and bust in their population dynamics (*45*, *46*). For example, after a climate regime shift in the North Pacific Ocean in 1989, Pacific herring (*Clupea pallasii*) and salmon (*Oncorhynchus* spp.) in the northern Bering Sea declined, whereas walleye pollock (*Gadus chalcogrammus*) in coastal Southeast Alaska increased; communities that had the required permits and gear could switch to catching walleye pollock and thus suffered little economic consequence of the regime shift (*43*). Similarly, fishers in the northeast United States switched to catching more fluke (*Paralichthys dentatus*) as hake (*Merluccius bilinearis*) became less abundant, buffering their revenues despite climate-driven changes to the abundance and distribution of these fishes (*44*). Given that climate change will shift the distribution of resources across space and time, legitimate policy options might allow exploiters to track transient harvest opportunities as they become available (*47*), instead of treating such opportunistic behavior as roving banditry (*24*). Like the dynamic habitat protection strategies described above, such harvesting strategies will require rapid assessment of emerging resources and a high level of control of exploiters to relieve pressure on species that become rare or unproductive.

Environmental decision-making and resource management strategies have a history of putting little emphasis on the future, and oncoming climate change necessitates a shift in this perspective. Myopic approaches to resource management often derive from the application of economic models that make strict assumptions through social discounting about the value of ecosystems, or the costs of restoring them, in the future. But future generations will bear nearly all of the brunt of ongoing climate change, even if we can rapidly reduce GHG emissions (*48*). When assessing the costs of protecting habitat now, versus the potential costs of damage to ecosystems that will be encountered by the generations in a climate-altered future, a lower discount rate is reasonable, particularly given the uncertainties of how the future of ecosystems will unfold (*49*). Given that different genes, populations, species, and habitats all provide options for an uncertain future, there is an increasingly urgent need to stem the rate of loss of these potential options. The approaches we have highlighted here may enable species and ecosystems to function and persist in a warmer future. These approaches place emphasis on future options for species and ecosystems rather than simply treating them as a commodity of the present.

Conclusions

Developing and implementing successful conservation science for a climate-altered future will require proactive application of existing and emerging approaches. The futures considered by humanity must be assumed to be different from what were experienced in the past, and these futures are deeply uncertain (*7*, *50*). Expectations should be for social, ecological, and evolutionary change, and science and policies should develop strategies for enabling change, monitoring it, and balancing the risks and opportunities it presents to the biosphere and humanity. Conservation approaches should facilitate evolution, dispersal, and compositional turnover in ecosystems. A fundamental stumbling block will be to reconcile such approaches that maintain community turnover while preventing extirpations of biodiversity that provide future options. Although scientific approaches may illuminate trade-offs in achieving each of these potentially conflicting goals under different conservation strategies, deep engagement with a diversity of stakeholders and the values they hold should ultimately point the way forward. In some cases, oncoming changes as well as proactive approaches will challenge common perspectives and values that were built on a baseline that was assumed to be stationary (*25*). Maintaining and restoring the processes that generate heterogeneity in habitats, genes, and communities should be prioritized for maintaining ecological options for the future. Thus, most of the conservation strategies needed to enable adaptation in species and ecosystems and to minimize climate impacts will play out at local to regional scales, even as reducing emissions of GHG to allow recovery of the climate system will require prompt global coordination. Climate impacts may completely overwhelm local actions, and actions may have unintended consequences that demand further adaptation. Regardless, even as humanity strives to reduce GHG emissions, there is urgent need to protect ecological options and enable adaptation of species and ecosystems to a shifting and unpredictable Anthropocene.

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ACKNOWLEDGMENTS

S. Wilson and D. Scurfield assisted with figure preparation. We thank the Gordon and Betty Moore Foundation for support and S. McClatchie and I. Hendy for sharing data. **License information:** Copyright © 2022 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. https://www.science.org/about/science-licenses-journal-article-reuse

Submitted 4 April 2022; accepted 19 May 2022
10.1126/science.abo3608

Science

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Jonathan W. MooreDaniel E. Schindler

Science, 376 (6600), • DOI: 10.1126/science.abo3608

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