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Who Should Pick the Winners of Climate Change?

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Abstract

Many conservation strategies identify a narrow subset of genotypes, species, or geographic locations predicted to be favored under different scenarios of future climate change. But a focus on predicted winners, which might not prove to be correct, risks undervaluing the balance of biological diversity from which climate change winners could otherwise emerge. Drawing on ecology, evolutionary biology, and portfolio theory, we propose a conservation approach designed to promote adaptation that is less dependent on uncertain predictions about the identity of winners and losers. By designing actions to facilitate numerous opportunities for selection across biological and environmental conditions, we can allow nature to pick the winners and increase the probability that ecosystems continue to provide services to humans and other species.

Managing Ecosystems for Adaptation

Earth's ecosystems are in a period of rapid change during which organisms are experiencing novel combinations of physical conditions, including altered temperature regimes, precipitation patterns, and water chemistry. We are already seeing the consequences of these changes as the earth begins a wholesale reshuffling of biological diversity. While the fields of ecology and conservation biology are increasingly focused on documenting and understanding these changes, there is a growing recognition of the need to make practical decisions about how ecosystems can be managed so that they can continue to provide ecosystem services under a range of future environmental conditions.

Populations and communities can adjust to novel environmental conditions through several processes, including geographic range shifts towards more suitable habitats, changes in demographic processes, physiological acclimatization, ecological reorganization, and natural selection (see Glossary). In conservation biology, much attention has been paid to anticipating range shifts by building latitudinal or elevational corridors to promote dispersal, sustain demographic processes, and maintain community interactions [1,2], and to facilitating range shifts through assisted colonization and migration [e.g., 3]. While these examples are promising, they focus primarily on the spatial redistribution of target species. We argue that greater attention needs to be given to managing for a more comprehensive consideration of adaptation, which we define to include the processes of acclimatization, ecological reorganization, and genetically-based evolution through natural selection.

Predicting the Future Versus Managing for Uncertainty

Many approaches to managing species in a changing climate are built on a predict-and-prescribe paradigm, whereby conservation priorities are based on predictions of the responses of species and communities to projected future environmental conditions. For example, assisted migration relies on predictions about the future distribution of organisms that are themselves based on predictions about the spatial distribution of future environmental conditions. Some predict-and-prescribe approaches are beginning to include considerations of adaptation. For example, on coral reefs there is a growing interest in creating ‘designer reefs’ [4] that might include ‘supercorals’ which have been artificially selected or genetically engineered for traits that are predicted to be more successful under future conditions of warmer and more acidic oceans [5].

One of the potential advantages of predict-and-prescribe approaches is that they offer a means of prioritizing actions to favor a set of predicted environmental change winners in the form of focal genotypes, species, habitats, and/or geographic locations. If the underlying predictions prove correct, this approach could be quite efficient and successful, and it can provide a more optimistic lens on the prevalent ‘doom and gloom’ forecasts of global change. However, by choosing a relatively narrow set of predicted winners, this approach risks erosion of the overall diversity within a system. Indeed, Schindler and Hilborn [6] have argued that predict-and-prescribe approaches are inherently risky and might achieve only limited success because they employ methods with intrinsically low predictive power, and typically consider only a narrow range of potential outcomes. This can help to explain consistent surprises in ecosystem responses to environmental change [7–9].

In financial markets, portfolio theory suggests that when faced with a variable and unpredictable future, it is risky to invest in a small number of stocks based on a narrow set of predictions; instead, the profitable response is to invest widely and maintain options for the expression of unanticipated favorable outcomes [10–12]. If predict-and-prescribe approaches have proven too risky for conserving monetary wealth, they are also likely to be risky for conserving ecosystems in the face of global change, especially because there is high uncertainty about how climate change impacts will play out at local scales, both in terms of environmental conditions and species' responses [13].

Based on a synthesis of core concepts from ecology, evolutionary biology, and portfolio theory, we describe an approach to natural resource management that focuses on creating adaptation networks explicitly designed to generate ecological and evolutionary options that favor the adaptive processes of acclimatization, natural selection, and ecological reorganization. By prioritizing portfolios of biological and ecological combinations, management could increase the probability that winning combinations can arise, persist, and spread during periods of environmental change.

Adaptation Networks: A Portfolio Approach to Managing Uncertainty

Adaptation networks could be designed around a suite of spatially explicit management units where actions are aimed at reducing local anthropogenic stressors. By reducing local stressors, these management units might provide some immediate local adaptive benefits, including increasing the probability of acclimatization, reducing mortality, and increasing reproductive output [14]. When these management units are part of an adaptation network, they are more likely to promote adaptation if they have (1) diverse portfolios, (2) connectivity between populations, and (3) metapopulation conservation and risk mitigation.

Diverse Portfolios

Evolutionary theory states that the amount of available variation is a key driver of adaptation [15]. Therefore, the processes of natural selection and ecological reorganization will be more likely to find successful combinations if they are operating on a diversity of genes, genotypes, phenotypes, and species. Across a landscape of diverse conditions, selection and environmental filtering can help maintain genetic and species diversity at metapopulation and metacommunity scales by favoring particular alleles or species in certain environments [16,17]. Extreme environments, where organisms might have already undergone local acclimatization and selection for physiological tolerance, could be especially important for this purpose [18]. Managing for portfolio effects has been applied to reforestation, wetland habitat conservation, and fisheries management under climate change [10,19,20], as well as reserve design to optimize natural capital and social equity [21].

Connectivity Between Populations

Given the rapid pace of environmental change, organisms have a small time window for adaptation. Genetic adaptation is most likely to occur via selection on pre-existing genetic variation rather than new mutations [22]. Therefore, the flow of genes between populations will be integral to rapid adaptation because it increases genetic variation at a local scale [23,24]. While connectivity can also have a negative influence on population fitness—by swamping the influence of an advantageous gene, or by transmitting deleterious mutations [25]—

environmental conditions are often strong enough to select and favor advantageous immigrants over deleterious ones in what is called a phenotype-environment mismatch [26]. Even in environments with high gene flow, substantial divergence of populations across environmental gradients is common and can occur rapidly [16,18,27]. Therefore, we can expect that climate change will provide strong selection pressure for advantageous combinations, even with high levels of connectivity between populations [28]. Ensuring connectivity among populations will also allow emergent areas of favorable environmental conditions to be colonized by surviving populations through metapopulation rescue processes [29].

Metapopulation Conservation and Risk Mitigation

Ensuring species are broadly distributed across a range of climate impacts will increase the probability that different populations and communities will experience different environmental conditions. Here, the objective is to promote weak or negative covariance in climate dynamics, allowing the metacommunity to achieve stability despite variability in its individual components. This is similar to optimizing financial portfolio performance through multiple investments [30,31]. In addition, broad spatial representation of populations and communities is expected to reduce the risk of metapopulation or metacommunity extinction from localized disturbances (e.g., storms), and protect against demographic stochasticity, which could become increasingly important as population sizes are reduced.

The combination of these three attributes creates an adaptation network that provides a diverse portfolio of evolutionary and ecological opportunities to find viable matches between biodiversity and future environmental conditions, without relying on predictions about winners or the distribution of climate change impacts. By facilitating the underlying processes of change through natural selection, acclimatization, and ecological reorganization, an adaptation network explicitly assumes that some aspects of biological diversity will be lost and that some adaptations will arise unexpectedly [32]. In this way, an adaptation network resembles a metacommunity or a complex adaptive system: though individual communities or system elements might be extirpated, the metacommunity and overall system remains viable [33,34].

Coral reefs: A Case Study

To illustrate how an adaptation network might be designed, consider the case of coral reefs. Coral reefs are one of the ecosystems most threatened by global environmental change, including ocean warming and acidification, as well as local stressors such as eutrophication and overfishing [35]. Contemporary observations and future predictions indicate that reef-building corals are experiencing steep population declines that threaten the foundation of these ecosystems and the services they provide [36]. Without significant adaptation, there are good reasons to question whether corals will be able to continue acting as the primary architect of reef habitats in the coming century.

There is growing evidence that corals can adapt to changes over relatively short time-scales through a variety of mechanisms that include symbiont shuffling, phenotypic plasticity, acclimatization, and natural selection [18,37,38], and some evidence to suggest that corals and their symbionts have already adapted to some warming since the onset of the Industrial Revolution [39]. Though they are long-lived, corals have a diversity of genotypes and phenotypes, as well as diversity in algal symbionts and microbial communities [16,40], which provides a potential treasure trove of raw material for adaptation. For example, a single species of coral can have a broad geographic range and populations spread across a mosaic of environments, from exposed forereefs to sheltered, warm lagoons, with differences in gene expression and allele frequencies between sites separated by tens of meters [41]. The impacts of climate change on corals are also spatially variable, providing diverse opportunities for biological and environmental matches and mismatches to occur [42,43].

Additionally, unlike many species, the ability of corals to respond to changing conditions through geographical shifts (e.g., by changing latitudes or depth) might be limited. While corals can exhibit rapid poleward movements toward cooler waters [44], higher latitudes have increased acidification and unfavorable seasonal variations in temperature and light [45]. Similarly, while tropical mesophotic reefs might have the capacity to act as depth refugia [46], deeper waters can be unavailable to many coral species due to the light levels required for their photosynthetic algal symbionts. Therefore, while some coral species might redistribute from one geographic region to another or towards deeper reefs, the overall persistence of shallow coral reefs—and the livelihoods of millions of people who depend on them—will require *in situ* adaptation to changing environmental conditions [18,47]. Future conservation efforts on coral reefs could build upon existing managed area networks (e.g., marine protected areas, locally managed marine areas, ridge-to-reef watershed areas) by placing additional emphasis on the three attributes of an adaptation network.

Diverse Portfolios of Corals

To ensure a highly diverse portfolio, managed areas could be deliberately chosen to encompass a range of environmental conditions—including extreme, variable, and stable environments—and include representation of many habitat types (e.g., lagoonal reefs, reef slopes, mesophotic reefs) under the expectation that phenotypic and genetic diversity are maximized across diverse environments [41]. In contrast, most current approaches to spatial management of coral reefs emphasize a disproportionate investment in 'pristine' areas, healthy reefs, and places that reduce social conflicts (e.g, 'residual reserves' *sensu* [48]). In addition, there is a growing movement toward protecting areas predicted to exhibit protective temperature trajectories, including climate change refugia [43,49]. While these areas should continue to be included in management portfolios, disturbed or impacted communities should also be considered for network inclusion as these sites could harbor species and alleles that will facilitate future adaptation. For example, these areas might contain weedier or more stress-tolerant species whose life histories enable more rapid adaptation [50,51].

Connectivity Between Coral Populations

To facilitate connectivity, management areas would be located sufficiently close to each other to permit the exchange of genes via coral larvae. Not only will this allow new genetic information to be acted upon by selection, connectivity will also allow populations to supply larvae to reefs where environmental conditions have shifted to approximate those of source reefs, i.e., metapopulation and genetic rescue [52]. Furthermore, the unambiguously negative effects of climate change on corals are expected to create strong selective forces [53], which might counteract potential costs of connectivity, such as gene swamping across environments or the immigration of maladaptive genes [17,25]. Operationalizing connectivity within the context of portfolio effects requires consideration of larval dispersal potential and gene flow, and recognition that future connectivity could differ from contemporary patterns [54,55]. Therefore, intra-network spacing that promotes abundant connections between communities will be an important attribute of adaptation networks that perform well under a wide range of future scenarios.

Metapopulation Conservation and Risk Mitigation on Reefs

Mitigating spatial risk would be accomplished by creating networks of managed areas at regional scales that function as metacommunities distributed across a range of environmental regimes [34]. The minimum size of such networks would be defined by the area required to ensure representation and replication of a range of environmental conditions (including thermal regimes, see [24]), and to reduce the risk that all populations could be extirpated by a single catastrophic disturbance (e.g., tropical storm). The maximum size of networks would be informed by the requirement that connectivity be able to facilitate adaptation to match rates of environmental change (i.e., corals need to adapt to climate change at the scale of years and decades).

Adaptation Networks in Practice

While networks of well-managed areas designed to cope with the uncertainty of climate change are not a novel concept [24], adaptation networks add a new dimension because they could be explicitly designed to promote the likelihood of adaptation via acclimatization, ecological reorganization, and natural selection [14,56]. Importantly, this strategy is in contrast to some predict-and-prescribe approaches, which use narrower predictions to prioritize conservation actions based on forecasts about specific locations or species that are more likely to be successful under future conditions, thereby potentially reducing the regional diversity captured within conservation areas. A priority for future conservation planning is to link adaptation networks into regional MPA planning by identifying gaps in existing MPA networks where new management actions should be prioritized to ensure networks include a diverse portfolio of interconnected options for adaptation [47]. In some cases, for example where gene flow limits local adaptation or facilitates the spread of maladaptive genes, more active intervention could be required for successful adaptation [52,57].

Currently, we have enough information to start developing and implementing adaptation networks for coral reefs and other biomes [30], and with the accelerating pace of environmental change, we have little time to waste. Modeling techniques that are currently being applied to problems like MPA network design or terrestrial conservation planning could be modified to design adaptation networks. These models have the potential to address some key outstanding questions (see Box 1), especially if they evaluate the potential advantages of alternative spatial management designs against a range of scenarios of future environmental conditions, within risk management and portfolio theory frameworks [37].

Implementing approaches to managing for adaptation will require regional leadership and collaborations between conservation NGOs, academic researchers, governments, and local stakeholders. In many cases, adaptation networks would likely span political boundaries, requiring transnational conservation strategies and agreements [58]. New approaches to conservation like these will require innovative policies that recognize the dynamic nature of systems, facilitate inter-governmental cooperation, and create opportunities for faster adaptive management [59,60]. For many ecosystems like coral reefs, conservation will likely continue to occur at local scales, where national governments are less likely to play a substantial role in natural resource management in the near term but could catalyze support for regional and transnational conservation networks. A key challenge will be to align local incentives and efforts with creation of regional adaptation networks that support ecosystem services while also promoting adaptation.

Concluding Remarks

Climate change and local impacts are creating immense challenges for species in terrestrial and aquatic ecosystems. We argue that the current focus of some climate adaptation approaches on predict-and-prescribe conservation strategies might be insufficient for meeting these challenges because they rely on inherently uncertain predictions to pick a small number of climate change winners. Instead, a more successful approach will be to develop networks that embrace existing portfolios of variability in environments, genotypes, species, and communities to provide a wide diversity of options. In other words, we need to protect biological diversity and let nature pick the winners.

Glossary

Acclimatization: a phenotypic response in which an organism adjusts to changes in its environment by altering performance through primarily physiological mechanisms; does not involve changes to genetic sequences.

Adaptation: the processes by which organisms and communities become better suited to environmental conditions through a combination of acclimatization, natural selection, and ecological reorganization (we recognize that the term adaptation has sometimes been more narrowly defined in the literature, e.g., only for genetic adaptation, but we use it here as a broad-sense term).

Adaptation network: a regional system of managed areas with attributes that promote adaptation; attributes include high diversity, connectivity, and spatial risk mitigation.

Ecological reorganization: changes in species composition within communities in response to changes in environmental conditions, which typically results in novel assemblages of species and traits compared to historical baselines.

Natural selection: the process by which allele frequencies within a population change through time as environmental conditions favor the survival and reproduction of organisms with certain genotypes; also known as genetic adaptation.

Predict-and-prescribe: an approach to conservation and management that prioritizes the protection of particular species, genotypes, and/or geographic locations based on predictions about future environmental conditions and their effects on organisms.

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