Opinion

Accommodating climate change contingencies in conservation strategy

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Species ranges are seldom at equilibrium with climate, because several interacting factors determine distribution, including demographic processes, dispersal, land use, disturbance (e.g., fire), and biotic interactions. Conservation strategies in a changing climate therefore cannot be based only on predicted climate-driven range shifts. Here, we explore conservation and management options in a framework for prioritizing landscapes based on two 'axes of concern': landscape conservation capacity attributes (percentage of protected area, connectivity, and condition of the matrix) and vulnerability to climate change (climate change velocity and topographic variation). Nine other conservation actions are also presented, from understanding and predicting to planning and managing for climate change. We emphasize the need for adaptation and resilience in populations, ecosystems, and the conservation environment itself.

A context for conservation action under climate change

Conservation strategies for climate change have focused largely on accommodating species range changes by maximizing connectivity and future climate space at higher latitudes and altitudes [1]. This strategy is supported by observations [2] and projected outcomes from a range of modeling approaches [3–5]. However, although a wealth of cases of poleward and ascendant movement have been documented [2], a recent meta-analysis revealed that, in 28 out of 30 cases, elevational responses lagged behind climate change and 25% of species moved downslope rather than upslope [6]. Furthermore, 22% of the taxa studied shifted their latitudinal range in a direction opposite to that expected [6]. In other studies combining the velocity of climate change (movement of isotherms over time) and the shift in seasonal temperatures, range shifts were not simply in the direction of higher latitudes and altitudes, but instead showed a complex mosaic of different climate and response velocities [7–9].

More cases of idiosyncratic, and sometimes unexpected, responses to climate change are being reported, as exemplified by recent evidence showing range expansion rather than expected contraction in a habitat specialist [10]. These findings are consistent with what is understood about the multiple determinants of species ranges and the contingent nature of species relations with climate [4,11] (Figure 1).

Intact ecosystems that retain their full complement of species are more likely to be buffered from the effects of climatic change by greater levels of functional redundancy, whereas degraded systems might be less resilient and more prone to trophic cascades [12–14]. Similarly, invasive species are hampering conservation efforts [15,16], thereby exacerbating the risks posed by climate change [17,18]. Such findings make it difficult to tease apart the relative influences of ecosystem change and changing climate on ecosystem resilience and to predict the distributional range limits of species [19].

The resilience of species to changing climate depends not only on the effects of disturbance [20] and biotic interactions [10], but also on their phenotypic plasticity and evolutionary potential [21–23]. Increasing climate variability and extreme events might, for example, select for genotypes with greater flexibility that confer resilience and the capacity to adapt [22]. Microevolution is also likely to be spatially heterogeneous and might be most likely at range limits, where genetic variation tends to be higher and where individuals with a wider climatic tolerance can reproduce more successfully [24].

Predictive tools have focused attention on the efficacy of conservation areas under climate change and are becoming increasingly sophisticated [5,25]. Complex models now incorporate a range of processes, including dispersal, physiology, population dynamics, competition, habitat change, and adaptation (Table 1). Nonetheless, accumulating cases of ecological surprise suggest that predictive tools are as yet unable to integrate fully the multiple determinants of species distributions. This raises significant challenges for conservation in a rapidly changing climate (Figure 1). Furthermore, to date there is comparatively little research on what the most effective management interventions are likely to be [26]. Maximizing connectivity and future climate space, although an invaluable strategy, is insufficient to deal with the contingencies of current and future biodiversity responses to climate change [1,27–29]. A more integrated strategy is required, which takes advantage of the full breadth of current understanding of species responses, survival probabilities, and range determinants, and that facilitates rapid and anticipatory conservation action.

Here, we discuss a suite of options for the conservation and management of biodiversity. First, we present a

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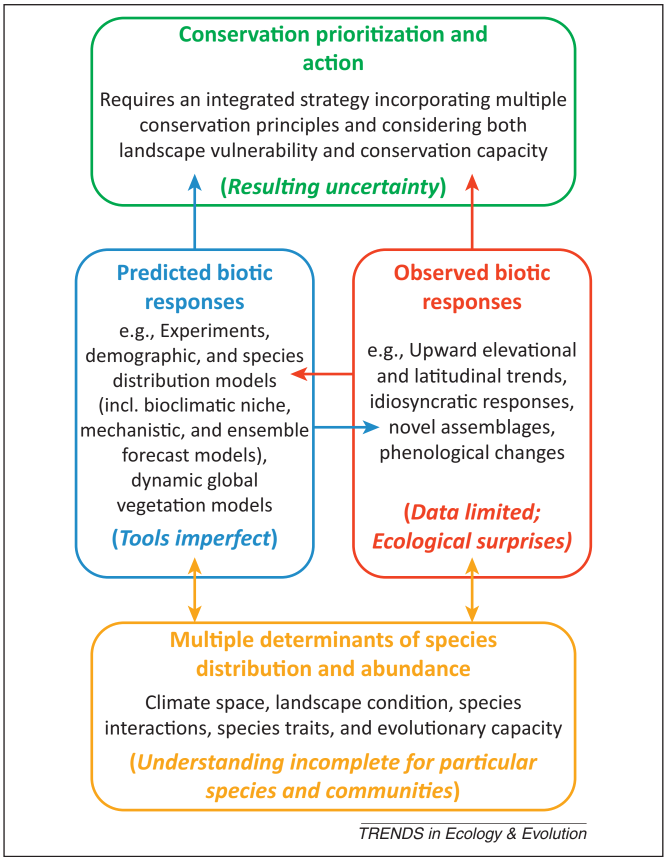

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Figure 1. Context in which climate change-related conservation action takes place where decisions are made on the basis of understanding the determinants of species distributions [14], predictive tools [5], and observed responses to climate change [2,6,10].

generic framework for first-level decisions based on landscape conservation capacity and vulnerability to climate change. This framework is then complemented by a range of nine other broad approaches to conservation that integrate a suite of actions, from understanding and predicting to planning and managing for climate change.

Complementary strategies for integrated conservation action

Identify priority landscapes using 'axes of concern'

When prioritizing landscapes for management intervention, important 'axes of concern' are landscape conservation capacity and vulnerability to climate change. Landscape conservation capacity attributes include the percentage of area protected, and the connectivity and condition of the matrix (i.e., the land outside protected areas), whereas landscape vulnerability includes rate of climate change (exposure) and topographic relief. The latter determines the range of available microclimates, hence affecting the likely resilience of populations to climate change.

These axes distinguish landscapes with varying responses to climate change and different requirements for planning and management [30] (Figure 2). Each landscape can be evaluated in the context of different exposures to climate change (i.e., the degree of change being experienced, *sensu* Dawson *et al.* [11]). For example, low exposure to climate change in a landscape that has attributes that confer resilience and high conservation capacity (top-left quadrant of Figure 2) can motivate greater investment in monitoring of threatened species in this generally low management intervention landscape. By contrast, reducing stressors other than climate is a common requirement across all landscapes (Figure 2, [31]).

Sensitive landscapes (lower-right quadrant, Figure 2) are those with poor conservation capacity combined with a high exposure to climate change (i.e., low percentage protected area, low connectivity, and large areas of degraded habitat, combined with low topographic relief and exposure to a high velocity or magnitude of climate change). Such landscapes have fewer microclimates and more movement is required in areas of low topographic relief to keep pace with shifting climate space. Hence, the focus must be on enhancing heterogeneity and improving the connectivity and quality of the matrix. An example of such sensitive landscapes are the biodiverse lowland fragments in the fynbos biome (South Africa), which are under-represented in the protected area network and are subject to higher land-use pressure because of their suitability for agriculture, and higher concentration of urban centers [32]. Susceptible landscapes with high conservation capacity (top-right quadrant, Figure 2) but high vulnerability also require management interventions focused on enhancing heterogeneity and resilience.

Similarly, in resistant landscapes (lower-left quadrant, Figure 2) with low conservation capacity, the emphasis would need to be on expanding protected areas, enhancing connectivity, and restoring the matrix. If areas of low climate velocity have high species endemism [9], then these species and areas must also be prioritized. In this framework, specific landscapes can be prioritized for action and a suite of conservation principles tailored to the landscape context.

Use scenario building to plan, research, and explore future options

The capacity of biodiversity to respond to climate change is both scientifically and socially uncertain (Figure 1) and a scenario-building approach is therefore useful to both research and management planning [33,34]. During scenario building, alternative conservation strategies for different combinations of climate change and, for example, biological adaptation capacity or land-use change, are formulated [35–38]. The process simultaneously promotes understanding across scientists, managers, policy makers, and other stakeholders [39].

Scenarios might be productively used to examine socially, ecologically, and evolutionarily uncertain outcomes, from which explicit hypotheses and assumptions can be developed and tested. This approach has been applied, for example, when designing reserve networks for coral reefs that accommodate uncertainty in genetic adaptation and phenotypic acclimation [40]. Scenarios that are plausible, but that also consider rogue events, which are possible but unlikely, [37] facilitate better understanding of ecosystem sensitivities, and potentially identify emergent system behavior and critical thresholds [41]. In this way, future management options might be planned for best- to worst-case scenarios, within a framework that is both anticipatory [42] and flexible enough

Table 1. Summary of modeling approaches that combine the effects of climate change, dispersal, land use, population dynamics, and other factors to predict the future distribution of species

Model	Description and example applications	Refs	Process							
			Climate	Dispersal	Physiology	Demography / population dynamics	Disturbance	Fragmentation, land-use change	Biotic interactions / competition	Adaptation (phenotypic and genetic)
Dispersal chains	Models climate and connectivity, prioritizing for protection 'dispersal chains' connecting present and future climate space; e.g., prioritization of dispersal chains for individual species of Proteaceae for the time period 2000–2050 across the winter rainfall region of South Africa	[43]	X	X						
Impacts of climate and land-use on Red List status	Models the Interacting effects of climate change and land use on Red List status; e.g., 66 taxa of Proteaceae would be uplisted if worst-case climate and land-use changes were considered together, compared with 25 species uplisted for land-use change alone	[35]	X	X		X		X		
Climate change and habitat suitability	Future suitable habitat modeled, including not only climate parameters but also plant species that provide shelter or food, as well as land transformation and availability of suitable habitat; e.g., habit availability for endangered riverine rabbit	[45]	X					X	X	
DRMs	Simulate how local demographic rates and population dynamics interact with climate and dispersal, to predict spatiotemporal variations in abundance and distribution; e.g., species not at equilibrium with climate (e.g., exotic invasives, r-strategists and rare species limited by postglacial expansion) can be accommodated in these models	[47]	X	X	X					
DGVMs	Predict the distribution of different plant functional types (classified by plant form and traits) incorporating competition and climatic parameters and, in some cases, plasticity in plant traits	[5]	X		X				X	X
aDVGMs	Models adaptations and plasticity in phenology, carbon allocation, and physiology in response to changing temperature, moisture availability, and disturbance, notably fire; e.g., the model suggests transitions of grasslands and savannas to forest vegetation at elevated ambient CO_2	[48]	X		X		X			X
Hierarchical	Determines how the effects of changing survival, growth, and reproduction manifest at the population level; e.g.; how plasticity in morphology, biomass accumulation, flowering probability, and reproductive effort can buffer the effects of climate change on demography and dispersal traits	[73]	X	X	X	X				X
Biomove	A novel modeling tool that includes competition, dispersal, and land-use change, as well as climate impacts; e.g., It simulates the persistence and range shifts of plant species in response to climate, habitat structure, and disturbance, at annual time steps	[25]	X	X				X	X	

to respond to changing threat levels, thus ameliorating the often 'crisis discipline' nature of conservation in practice.

Use a suite of modeling techniques and integrate hierarchically across scales

Niche modeling remains a cornerstone of climate change-integrated conservation strategies. However, it is correlative rather than mechanistic and is often (although not exclusively) broad-scale, whereas many conservation decisions take place at the population level (i.e., on local to landscape scales). Many factors affect species distributions and new modeling approaches are now incorporating multiple interacting processes, including dispersal, land-use change, habitat fragmentation, and suitability [35,43–45] (Table 1).

Mechanistic or process-based models [11,46] relate the dynamic effects of climatic parameters, including extreme events and rates of change, on physiology and thereby changes in key population parameters such as fecundity and mortality [3,5,44]. Dynamic range models (DRMs) predict spatiotemporal variation in abundance and distribution [47], whereas dynamic global vegetation models [DGVMs and adaptive (a)DVGMS] predict the distribution of different plant functional types (classified by plant form and traits) incorporating competition and climatic parameters [5,48].

Models that integrate processes across scales are now emerging, for example, hierarchical models [3] and 'Biomove' [25]. Fully integrated models, including landscape genetics and microevolution, are within reach computationally, although they are data hungry and will require the collaboration of citizen scientists to gather time-series data across the entire distribution of a species [49].

Develop protected area networks and configurations that consider future climate space

Area-based strategies that accommodate biodiversity responses to climate change incorporate climate change design principles into systematic conservation planning [4]. Three explicit design principles are used: identification of the geophysical stage (diversity of topographies and soils); identification and protection of climate refugia; and maximization of cross-environment connectivity (also see following section) [50]. The outcomes of these tools are then used in integrated land-use planning at multiple scales [11,26]. For example, Pyke [51] used climate change design principles to identify new areas for protection that would better accommodate Proteaceae species in the Cape Floristic Region by 2050.

Including the widest possible altitudinal range within protected areas will preserve a greater variety of microclimates, and protecting areas of greatest abiotic diversity in terms of geology, soils, topography, and hydrology will further enhance habitat diversity [36,52]. Regarding reserve configuration, single large reserves are not necessarily the best option for a changing climate, because: (i) for the same habitat area, a biologically connected network of habitat patches covers a larger space, thereby extending the potential climate space [53]; (ii) a string of reserves arranged linearly over a climate gradient might preserve more future climate space; and (iii) multiple reserves spread extinction risk across populations and are more resistant to threats, such as pathogens and invasive species [53]. Paleoecological and genetic data can help in identifying climate refugia and important reservoirs of adaptive capacity [23,54]. Insight into individualistic responses and the speed of migration movement can inform how closely spaced reserves need to be if species are to track suitable climate space [9,55].

Increase the permeability and functional connectivity of the matrix

The potential for expanding protected areas is finite and effective management of the intervening matrix is critical for enhancing connectivity and maintaining genetic variability [56]. Management to increase connectivity includes, for example, restoration of riparian corridors or hedgerows [26]. Connectivity between populations is not simply a function of geographical distance, because the quality of matrix might differ in structure, configuration, and permeability. Permeability can be enhanced by combining a mosaic of land-use types, such as buffer zones around protected areas, agroforestry, silviculture, and areas of relatively low grazing pressure [30]. The persistence of metapopulations and the rescue of locally declining or extirpated populations depends on the ability of individuals to move between areas of suitable habitat. Once new habitat is reached, the chances of persistence in a fragmented landscape might be enhanced by increasing patch size, improving habitat quality, restoring vegetation, or slowing down rates of change [57,58]. In forests that are harvested on a rotational basis, for example, a longer rotation has been shown to be critical for population persistence [59]. Thus, both spatial and temporal factors are important considerations in maximizing functional connectivity.

Amelioration: use fine-scale management interventions to ameliorate undesirable ecosystem change

Hedging management strategies aimed at spreading or accommodating risk are particularly appropriate when expected changes are foreseeable but uncontrollable [33]. This is applicable at the scale of individual reserves or landscapes, where managers do not have the option of planning systematically for protected area expansion and connectivity across regional scales. Such fine-scale strategies include provision of habitat refuges, increasing habitat quality, managing herbivore and predator abundance, re-introduction or augmentation of populations of ecosystem engineers or keystone species [30], and manipulation of fire and grazing.

These interventions act at the population level, and populations under multiple stressors are likely to be less resilient in a changing climate [26,60,61]. Management interventions for stressors other than climate change are therefore critical at this scale. Aggressive prevention and control of alien invasive species is one such intervention, as is controlling upstream pollution, preventing overharvesting, and managing the permeability of boundaries [34,42]. Anticipatory management that safeguards viable populations and maintains habitat quality is an important part of the toolbox of responses to dealing with climate change-related contingencies.

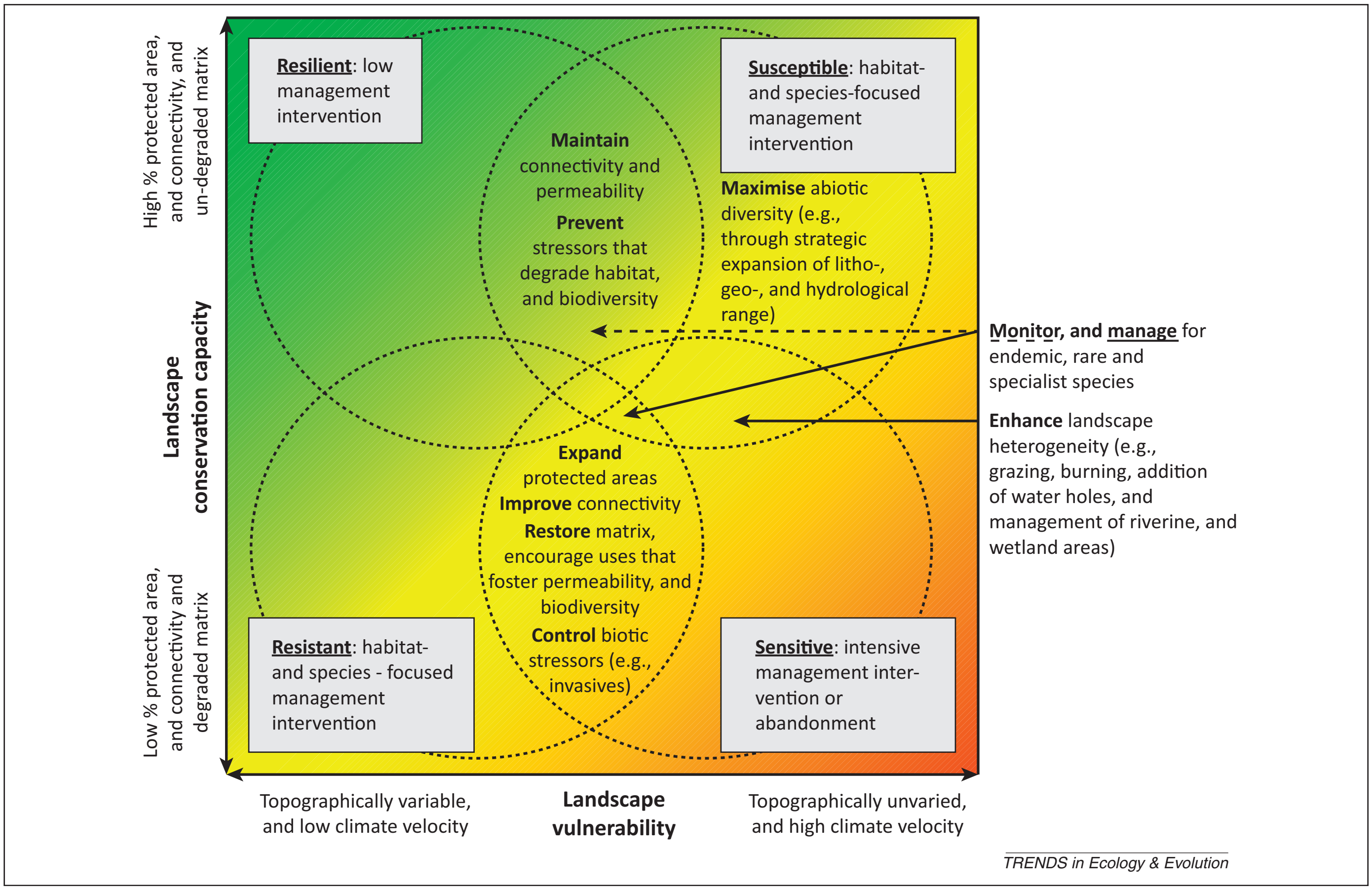

Figure 2. A conservation strategy based on two axes of concern. Landscape conservation capacity attributes (percentage protected area, connectivity, and condition of the matrix) and landscape vulnerability (exposure to climate change as a consequence of climate velocity and topographic relief) generate four principle conditions of varying landscape sensitivity and required level of management intervention, each requiring the application of a somewhat different suite of the most relevant, established conservation principles.

Maintaining a specific suite of species might not be possible at the level of an individual reserve [27,30,36]. The emphasis should then shift towards conserving the processes that build and conserve adaptive capacity, for example by maximizing genetic and phenotypic variability and enhancing the likelihood of population persistence and migration through boundary permeability and buffer zones. Finally, adaptive capacity within management frameworks and institutions (see below), which allows for timely responses to emerging information, as well as the ability to reformulate management goals or hypotheses, is key to effective amelioration of rapid, unexpected ecosystem changes.

Prioritize vulnerable species and enhance evolutionary potential by translocation and ex-situ conservation

Identifying the species most vulnerable to climate change requires the integration of past and present responses to climate changes, including historical and paleoecological data on rates of species migration, and the thresholds at which local extirpations occur [5,11,44]. Interacting factors such as changing land use will affect species extinction risk [35], as will variability in climate via impacts on fitness and species performance [62]. Data on genetic variation and evolutionary potential of the species are also required [23]. Multiple sources of information might thus be used to identify species that are unlikely to reach their future climate space naturally, either because of geographical isolation, or because their rate of dispersal or evolutionary potential is too low for current rates of climatic change, or because other stressors make their dispersal or even survival unlikely [29].

Where populations can be translocated, selecting individuals with broad phenotypic plasticity and from high latitude and altitude populations might enhance chances of individual survival and population persistence [42]. However, the evolutionary potential of translocated populations should also be considered [21]. Small pioneer populations at the leading edge might contain individuals with good dispersal abilities, but other adaptations might be missing and small populations are at risk from Allee effects [24,28]. Best practice for augmenting or rescuing existing populations could therefore be to source most translocated individuals locally, but include some individuals from more distant populations, thereby simulating a rare, long-distance dispersal event, a procedure termed ‘composite provenancing’ [63,64]. At the lagging edge, too much connectivity might swamp microevolution and adaption in refugia and, thus, a different strategy with less genetic pooling might be desirable [65]. In each case, the decision whether to translocate must consider the risks, costs, benefits, and feasibility [28–30,63]. Species facing imminent extinction might also need *ex-situ* conservation, for example, seed, sperm, and egg banks, botanic gardens, and arboreta [26].

Adaptation: manage adaptively for resilience and change

Adaptive management involves treating management interventions as experiments, the outcomes of which are monitored and fed back into management planning [1,30,36]. Such an approach is essential when uncertainty is high and decisions urgent, a situation currently faced given the range of possible future climate change scenarios [66] and the possibility that changing biotic interactions, trophic cascades, alien species, and pathogens might lead to ecosystem reorganization and novel communities [2,6,36,67].

Building on the scenarios outlined above, adopting an adaptive management approach will involve selecting and monitoring the outcomes of feasible management interventions. Management intervention within individual reserves can be adaptive, but adaptation is also needed at a strategic regional level. Where possible, replicate populations or ecosystems at the same latitude and altitude could be managed differently, for example, in terms of differences in land use or the intensity of intervention (e.g., relocations or assisted migrations) [68]. At large spatial scales, where ecosystem shifts are slower and more costly to monitor, adaptive management might be unfeasible, but can form part of a broad evidence-based approach (see below) [34].

Build adaptive institutional capacity, linkages, and knowledge networks across spatial and temporal scales

Despite the high uncertainty associated with future climate predictions, urgent decisions and rapid action are required to conserve biodiversity, including the genetic diversity that is needed for evolutionary adaptation. Various forms of information are available to decision makers, including the outputs of model simulations, long-term monitoring plots, paleoecology, and historical data [39]. Furthermore, multiple stakeholders have different views of ecosystem change and myriad agencies make conservation decisions at a range of spatial scales.

Capitalizing on this wealth of information and experience to benefit conservation will demand new forms of institutions and governance systems. These will be adaptive, polycentric, and multilevel in design to facilitate greater emphasis on understanding ecosystem dynamics and social–ecological interactions through improved analytical and modeling approaches [69]. The key elements for the adaptive governance of socio-ecological systems required under climate change include legislation that enables rapid response to change and unexpected events, flexible institutions, and interorganizational collaboration [69]. Environmental decision making needs to be sufficiently informed, flexible, communicative, and participatory to maximize responsiveness to both the risks and opportunities provided by the rapidity and increasing frequency of extreme events that characterize modern climate change and its consequences [69].

Build the evidence base for conservation action

The urgency and uncertainty associated with designing conservation responses to climate change necessitate the broad suite of approaches outlined here, particularly those that provide predictive forecasts that guide action. The bedrock of conservation response to changing environments will, however, continue to be evidence-based demonstrations of how ecosystems are changing and how effective policy and management actions are in ameliorating the effects of climate change. The integration of field surveys, field and laboratory experimentation, along with modeling and observation, monitoring, and assessment remains the most powerful approach upon which to base climate change-related response decisions [11,33,70]. A hypothesis-testing framework has recently been proposed that draws upon fundamental ecological and evolutionary theories and the evidence base to explain long-term population responses [71]. The outcomes of adaptive management might successfully be incorporated into such an integrated approach, especially in instances where the response being addressed is localized, short-term, and controllable [33,34].

Online open-access databases that are responsive to new observations, including data collected by citizen scientists, and open for meta-analysis, are likely to become increasingly important tools in evidence-based conservation. Good examples of this approach are the South African Bird Atlas projects, which use mass participation, long-term monitoring, and statistical modeling to contribute to the understanding and conservation of bird populations [72].

Towards integrative outcomes

To date, the emphasis for conservation in a changing climate has been on expanding protected area networks to accommodate future climate space, based on range shifts predicted by bioclimatic species distribution models, together with the establishment and strengthening of habitat corridors and stepping stones to facilitate dispersal and migration. Increasingly, however, the capacity to react to a range of different scenarios, sensitivities, and ecological surprises will have to be accommodated [6,11]. Building resilience in both ecosystems and institutions is therefore essential. Here, we have integrated advances in modeling and adaptive planning into a landscape framework, with the aim of guiding action that builds and maintains ecological resilience and evolutionary potential at a range of spatial and temporal scales. We are acutely aware that implementing such recommendations often will be hampered by insufficient capacity, financial, and logistic constraints, as well as organizational and administrative inertia. Nonetheless, integrative frameworks are an essential component of using the resources available rapidly and effectively, and moving towards an anticipatory rather than crisis-driven response to conservation in a changing climate.

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