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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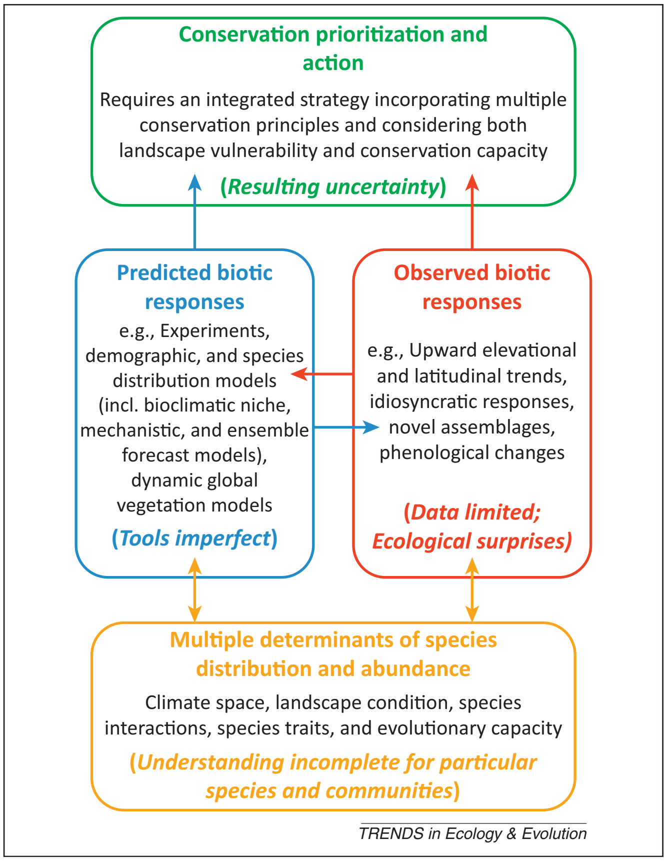

Figure 1. Context in which climate change-related conservation action takes place where decisions are made on the basis of understanding the determinants of species distributions [14], predictive tools [5], and observed responses to climate change [2,6,10].

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