PNAS SPECIAL FEATURES: INTRODUCTION

The past as a lens for biodiversity conservation on a dynamically changing planet

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We are in the midst of a major biodiversity crisis, with deep impacts on the functioning of ecosystems and derived benefits to people (1, 2). But we still have time to pull back. To do so, it is imperative that we learn from plants' and animals' past actions (3, 4). Conservation biology, ecology, and paleontology all emphasize that natural systems must exhibit resilience and dynamic responses to rapid environmental changes (3, 5, 6). Both climate and land-use change have accelerated over the past decades, underscoring the urgency for increased understanding and action (7–9). The cumulative effects of these disruptions are not additive or systematic; rather, they pose complex, dynamic environmental challenges to ecological systems (see "dynamic systems" Table 1). With the dramatic ecological effects from climate fluctuations and increasing instability of the fabric of life (10–12), we anticipate that biota will dramatically shift their ranges, reconfiguring ecological communities across Earth's natural landscapes (13) (Fig. 1). Today's most prevalent conservation approaches focus on the maintenance of static reserves. These approaches need to be supplemented by approaches that facilitate dynamic ecological shifts using flexible strategies that involve local stakeholders (14–17). In addition, given the magnitude, rates, and complex interactions of anthropogenic and climatic change occurring today, these conservation approaches must be informed by research that spans time scales to infer likely responses (18). This special feature integrates research from across spatial and temporal scales to explore how ecosystems and communities function dynamically to respond to large-scale environmental change, highlighting proposed solutions for conserving biodiversity on a rapidly changing planet (Fig. 2).

To accommodate migration, adaptation, and acclimation in response to rapid change, we must formulate effective, long-term dynamic conservation approaches. These involve the protection and restoration of resilient landscapes (Table 1) that can serve as regional climate refugia, allowing plants and animals to shift locally to acclimate to changing climates (18, 39, 40). Once climate change is extreme enough that the buffering capacity of these regional climate refugia is exceeded, plants and animals will need to traverse broader landscapes, requiring larger-scale ecosystem connectivity (17, 39, 40) (Table 1). Simultaneously, effective ecological restoration (Table 1) strategies must maintain ecosystem function, allowing primary productivity to continue and diverse taxa to persist despite ongoing geographic shifts and taxonomic turnover. The restoration of landscapes and conservation of individual species requires integrating the rapidly shifting environmental, social, and political landscapes into our risk considerations and engaging with local stakeholders (Fig. 2) to ensure success (16, 41, 42).

Given that 75% of terrestrial landscapes are strongly affected by human impacts while simultaneously undergoing rapidly changing climates (1, 2), there are many outstanding ecological questions that need to be addressed to identify the most effective dynamic conservation strategies. For example, although we anticipate that species will need to shift their ranges to track changing climates (43, 44) (Fig. 1), we do not know the extent to which individual species shift their ranges as ecosystems rapidly turnover (45) versus exhibiting climate flexibility, acclimating or adapting in place (46). Neither do we know the extent to which those species are influenced by different types of anthropogenic landscape changes (47–49) (Fig. 1). Biodiversity of all sorts, including functional diversity (Table 1), is decreasing as populations are extirpated and community compositions change (50). Functional traits (Table 1) have been used as indicators of past ecological function and environments due to their fidelity of signal. But as traits are lost within a community, ecosystem functions will likely shift due to offsets in those trait–environment relationships. However, we do not know the degree of diversity or combination of species traits that are necessary to maintain ecosystem function (51).

To address questions relevant to conserving biodiversity in the face of these large, dynamic, changes, we need to understand complex, large-scale interactions. This brings several challenges, notably that we must consider ecological responses over varying spatial and temporal scales in a rapidly changing system. Studies that expand over longer timescales can test hypotheses and models based on ecological principles using empirical data from past events (Fig. 2). Best practices mean knowledge coproduction of both questions and models for addressing conservation needs (52–54) and reporting of findings that can be easily translated for conservation applications (55) (Fig. 2). In this way, studies that span multiple spatiotemporal scales can serve to refine and refocus on-the-ground efforts for conserving biodiversity in a dynamically changing landscape.

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Table 1. Key concepts and terms as used in special feature articles

Key concept	Definition	Special Feature Article
Dynamic systems	"A theoretical framework that is used to understand and predict self-organizing phenomena in complex systems that are constantly changing, reorganizing, and progressing over time" (19)	This paper
Resilient landscape	A landscape that sustains "biodiversity and ecological functions over time in the face of climate change and other anthropogenic and natural stressors" (20)	(21)
Ecosystem connectivity	The capacity of habitat configuration to allow the "unimpeded movement of species and the flow of natural processes that sustain life on Earth" (22)	(21)
Ecological restoration	The process of reinstating communities to support ecosystem functioning and services, ecosystem connectivity, and biodiversity (23, 24)	(25)
Functional diversity	The "number, type and distribution of functions performed by organisms within an ecosystem" (26)	(27)
Functional trait	A "measurable property of organisms … that strongly influences organismal performance" (28, 29)	(27, 30, 31, 32)
Climate fidelity	The ability of a taxon to shift its range to track their realized climatic niche as climate changes (33)	(33)
Functional redundancy	The relative number of organisms that "occupy the same functional space" within an ecosystem (34)	(27, 30)
Ecometrics	"The study of the distribution of functional traits within and between communities in relation to environment"	(31, 32)
Effect size	A statistical estimate of "the magnitude of an effect" or the "biological importance of the effect" (35)	(36)
Socioecological gap	A geospatial representation that "includes both threat and resource components to determine if existing capacities are sufficient to promote stable geographic ranges" (37)	(37)

The aim of this special feature is to capture approaches that transcend fields. Conservation practitioners highlight the latest dynamic conservation strategies, which underscore the ecological theory and hypotheses that should be examined to effectively translate historical findings into actionable conservation practices. Ecologists and paleoecologists, working across temporal scales, demonstrate approaches that have already begun to effectively inform the conservation of biodiversity on a dynamically changing planet. Studies herein identify resilient and connected landscapes, explore ecological movement dynamics, and evaluate how extinctions and range-shifting species lead to the erosion of functional groups that affect trait–environment dynamics through space and time (Fig. 1). It is clear that we need to continue identifying a path forward for the meaningful integration of approaches across fields for the conservation of biodiversity and ecosystem function. Ecosystem preservation requires a clear understanding of trait–environment relationships across trophic levels. We highlight work from across a series of trophic levels from plants to herbivores to carnivores to demonstrate the strategies being used to assess how functional groups within ecosystems are structured, and the major drivers of change.

Connected and Resilient Landscapes

Today's changing planet presents challenges for conservation strategies. Previously, when climate or land availability changed dramatically, for example, during previous glacial–interglacial cycles, plants and animals traversed the landscape without experiencing the resistance that results from our highly fragmented and human-impacted landscapes (Fig. 1). Although both species' geographic ranges and ecosystem compositions have changed substantially in the past, overall biodiversity persisted in ecosystems often without a current analog or within climate refugia (13, 56, 57). Projections of migration requirements in the future compared to those of previous glacial-interglacial cycles show that much-accelerated migration velocities will be required to reach the nearest climate refugia (58). Additionally, given the extent of terrestrial human impacts (2), both climate refugia and migration tracts are being extensively impinged (38, 59) (Fig. 1). Identifying strategies to allow plants and animals to navigate this dynamic landscape requires conservation strategies that recognize and integrate the complexity of these issues in a spatially and socially explicit way.

As species ranges are encroached upon by new climate regimes and expanding human impacts, plants and animals will need to shift their ranges to track suitable habitats as they have done in the past (61, 62). To facilitate this, Anderson et al. (21) demonstrate a new framework for characterizing modern landscapes that promotes both landscape resilience and broader connectivity. The resultant maps will serve as a crucial tool for conservation prioritization in a changing world. The authors pinpoint places in the modern landscape where resilience to changing climates is highest. Diverse topography, bedrock, and soil are used to characterize high

Fig. 1. Species will need to shift their geographic ranges in response to rapidly changing climates (transparent red arrows). However, anthropogenic landscape features—such as cities, farms, roads, fences, and power lines—can act as filters or barriers necessitating alternate paths (solid red arrows). These features and other impacts can lead to geographic range contraction (e.g., imposed on taxa with only transparent arrows). Figure by Duncan MacGruer.

landscape resilience that will sustain biodiversity and ecological function into the future. They consider how habitat configurations promote the regional movement of plants, animals, and whole ecosystems. Conserving these areas will ensure that our dynamically changing planet harbors the climate refugia of the future.

Global human footprints are expanding because human needs are expanding. Thus, we must develop more nuanced strategies for considering both the threat to plants' and animals' ranges and potential directions forward for maintaining those species. This means working with a variety of landowners, land users, governments, agencies, NGOs, and conservation organizations (60). Public perceptions play a strong role in the ability of these groups to achieve their goals. For example, the public's fear of and negative associations with carnivores makes full trophic restoration challenging in some areas. Harris et al. (37) introduce the next generation of species-level gap analysis that considers these global dynamics. Their work integrates not only climate and environmental changes into species protection consideration, but it also considers socioecological threats and resources that could affect how species are protected to identify any socioecological gap (Table 1). When this is applied to 91 African carnivores, they find that the threats of range contractions are on average 15% more extreme than previously thought, yielding many suggestions for shifts in the threatened or endangered statuses of carnivores, particularly for smaller carnivores. But more importantly, this work identifies potential social and political partners to help conserve threatened carnivore species.

Identifying the spatially explicit vulnerabilities of individual species and protecting resilient and connected landscapes to allow those species to adapt to global change dynamics are important steps for conserving biodiversity. However, to effectively support these strategies, we must continue to identify intrinsic species traits and extrinsically driven dispersal and migration dynamics that will affect how, when, and if they will need to respond to dynamic environmental changes.

Ecological Movement Dynamics

Climate is a critical component for predicting where species are geographically distributed (63, 64). Because the climate is changing so rapidly, we assume that plants and animals will need to shift their distributions across climate gradients to track those changes (65, 66). However, although we know that both plants and animals have previously shifted their distributions to track climate, we also know that climate tracking often lags behind climatic changes (67, 68). Some organisms, in fact, possess distributions that are not directly affected by climate (69). Lags could result from dispersal limitations, particularly in long-lived plants, and today may be further limited by increasing habitat loss and fragmentation (49, 70). An essential challenge for evaluating species' responses to environmental changes is that it may take tens to thousands of years for geographic range shifts or other adjustments to occur (71, 72). To effectively predict the future movement needs and capabilities of plants and animals, we must integrate a temporal component into our assessments.

Identifying the geographic dispersal challenges faced by plants has been difficult for ecologists because most studies are conducted across relatively short time scales (days, weeks, months, or years). Ecological dynamics resulting from multiyear and decadal fluctuations in climate and management practices require a longer temporal perspective. Orrock et al. (25) report findings from a near-decade-long regional experiment to identify taxa, ecosystems, and their characteristics that benefit most from connected landscapes. They conducted a long-term and large-scale replicated experiment across the southeastern United States, manipulating seed arrival and neighboring competitors to evaluate joint impacts of timber densities, prescribed fire strategies, soil conditions, and climate on establishment and persistence. Species establishment and persistence dynamics depend on arrival, dispersal, and migration capability, potentially confounded by neighboring competitors. Orrock et al. (25) identify specific plant traits and environmental conditions that promote resilience under changing climates, maximizing conservation and restoration potential. Notably, they find that the strongest factor to influence plant establishment is seeding, or the presence of seeds in an area, while warming temperatures inhibit establishment. These findings point to the need for relatively long-distance climate tracking with warming, but a high potential for success given sufficient dispersal.

Orrock et al. (25) identify how to best promote climate tracking in plants, whereas Wang et al. (33) evaluate the extent to which different taxa have geographic ranges that will be strictly dictated by climate. To construct a comprehensive plan for responses to global change, we need to

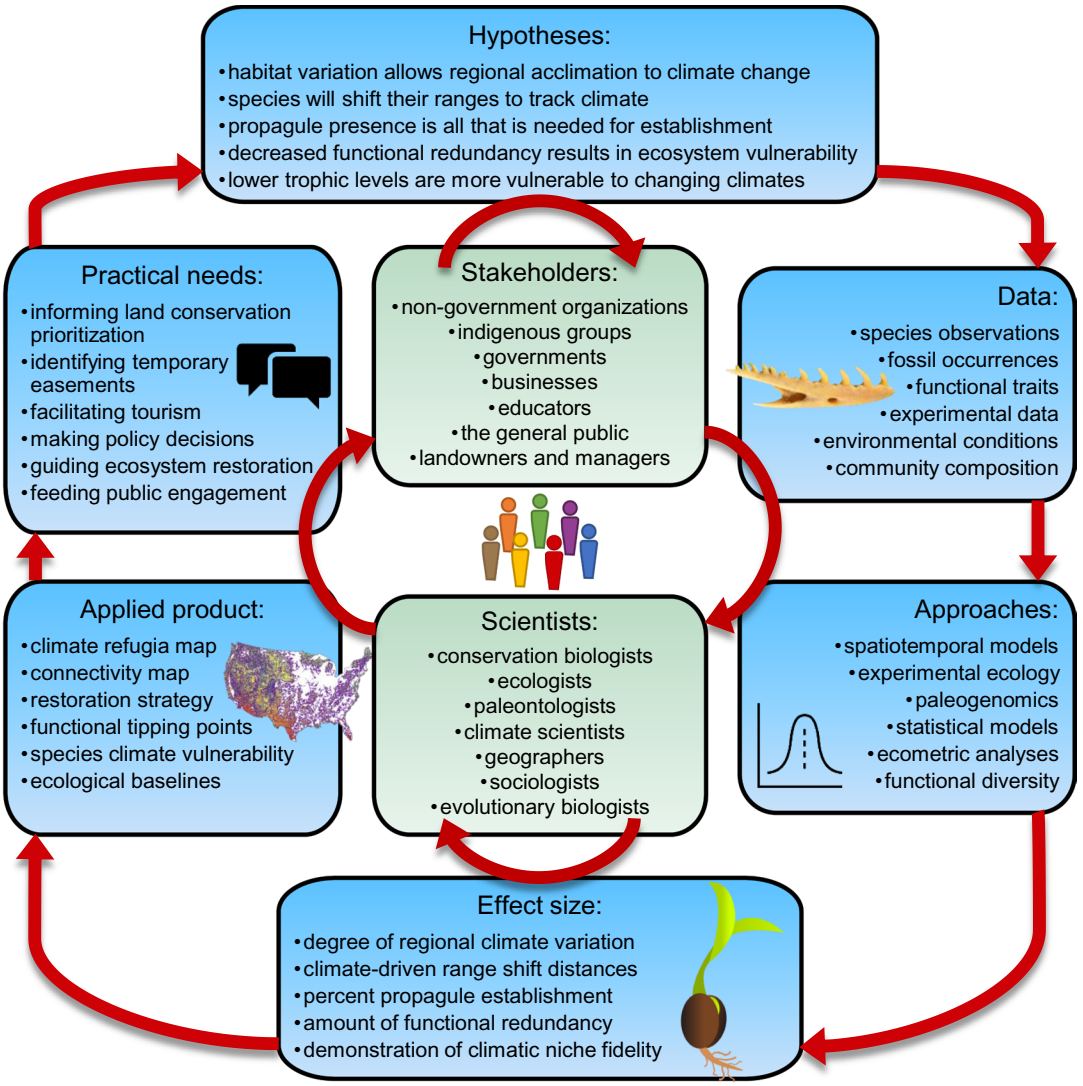

Fig. 2. Knowledge coproduction occurs through dialog between stakeholders and scientists. Together, they select the appropriate data and approaches to determine applicable effects, which are translated into applied products that can inform the practical needs of stakeholders. Images, from top-right: a fossil snake dentary, a statistical model, a seedling indicating propagule establishment rate, and a map of possible corridors to facilitate climate tracking (modified from ref. 38).

evaluate which taxa exhibit climatic niche fidelity (Table 1) versus climatic niche flexibility (33, 46). These questions will help focus our efforts on those taxa that will be most affected by changing temperature or precipitation patterns versus those that may be more affected by other components of its niche, including biotic interactions or other abiotic components. Wang et al. (33) introduce a climate fidelity metric, which captures the degree to which species maintain their climate niches through time. They evaluate climate fidelity in North American plants over the past 18,000 years using the palynological record. They find that 75% of plant taxa exhibit high climate fidelity. These species have tracked climate for 18,000 years through relatively rapid changes in climate; they will require resilient and connected landscapes to keep doing so into the future.

Erosion of Functional Groups

As plant and animal communities are geographically shifting and reconfiguring in response to global change, so too do the traits and the functional diversity conferred by component species (28, 73). These changes happen locally as a result of redistributions or extirpations and globally due to extinctions. Given that roughly 25% of vascular plant and vertebrate species are currently threatened with extinction (2), functional diversity will continue to be eroded. Understanding the mechanisms underlying the loss of global biodiversity is critical for its conservation and the preservation of functioning ecosystems.

Over the past million years, glacial–interglacial cycles led to rapid expansions and contractions of ecosystems as they experienced considerable changes in both temperature and precipitation across the Northern Hemisphere (74). Germain and colleagues (27) evaluate the relative abundances and functional diversity of global bird clades over the past million years in response to these large-scale environmental changes. They find that functional diversity of bird species alive today, overall, has changed very little. However, there has been a gradual loss of functional groups in some of the more divergent aspects of trait space, specifically the loss of birds that exhibit more unusual trait sets, especially large-bodied birds that lay many large eggs (27). The losses

of these traits that have been previously associated with hunting or predation by invasive species, implicates potential anthropogenic drivers, and pinpoints historically vulnerable clades (27). Given that this trait set is energetically costly, they may be the harbinger of losses to come as birds continue to experience increased stress from increasing global change.

This slow erosion of functional trait spaces can be contrasted with work by Kemp (30), which evaluates how the functional diversity of Caribbean reptiles changed during the late Quaternary. When evaluating functional diversity at these smaller spatial and temporal scales, Kemp finds that the number of functional entities (functionally distinct species groups) has decreased by 70% on small Caribbean islands, a much more rapid and dramatic loss than observed in the global bird dataset. Reptile functional trait losses dramatically decrease the resilience of these small islands' ecological function and community-level adaptability to global change. However, on those small islands with few human occupants, functional entities are maintained. Large islands exhibited sufficient functional redundancy (Table 1) to maintain a larger pool of functional diversity. These findings highlight the need for maintaining resilient systems through the preservation of functional entities and restoring those functional entities when possible.

Biotas tend to become more homogenous in areas of high human impact through the extinction of native species or the introduction of nonnative ones (75). Often species within functional groups at the highest trophic levels (e.g., predators) are more sensitive to land conversion, habitat destruction, and fragmentation (49, 76). Similarly, species with larger body sizes, compared to small-bodied species, are more likely to be lost (77), which has led to missing portions of ecological space (78). Areas of high human impact have distinctive influences on different types of functional groups (79). Both of these articles find evidence of anthropogenic impacts in restructuring functionality within biotic systems, either through land-use conversion or direct harvesting. In both reptiles and birds, shifts in functional diversity, whether slow or fast, thus far appear to be driven by human land use and exploitation rather than changes in climate. Understanding how anthropogenic impacts restructure functionality within biotic systems will increase our understanding of the ecological consequences of biodiversity loss.

Trait–Environment Dynamics through Space and Time

Functional trait losses have important implications for overall ecosystem function, which can be assessed by evaluating trait–environment relationships for communities (Fig. 3). For example, the loss of grazing species with high-crowned teeth, which are adapted for consuming coarse plants in harsh environments, can theoretically affect the relative abundances of the plants growing in certain ecosystems, altering overall ecological function (80, 81). However, the complex interactions between functional groups, global environmental change, and ecosystem function require much more extensive investigation. Two papers in this special feature use a compelling approach, ecometrics (Table 1), for contextualizing consistent and disrupted trait–environment relationships

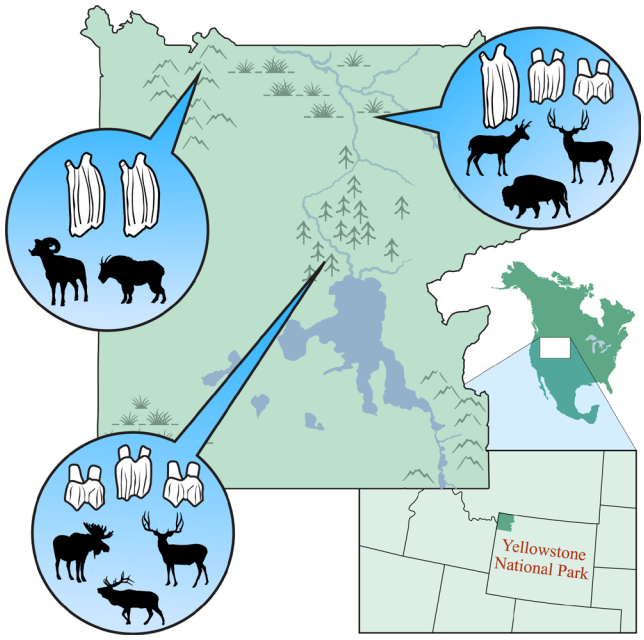

Fig. 3. Equilibrium communities possess traits that are well suited to the habitats where they are found. For example, bovids in Yellowstone National Park, Wyoming, United States, possess teeth that effectively process plants in their habitats. Mountain goats and bighorn sheep have high-crowned teeth for eating coarse, gritty grasses found on mountain tops. Moose, elk, and deer have lower tooth crowns, needing less durable teeth to process foods in forests. In addition, the mixed habitats around river systems are occupied by a variety of taxa, including pronghorn, bison, and elk. Figure by Duncan MacGruer.

(82–84). Parker et al. (31) and Short et al. (32) examine how well community-level functional traits align with the environments where they are found as change occurs across space and through time.

Physiological models of the mechanistic relationship between body size and temperature have been useful tools for estimating paleotemperature and evaluating functional trait–environment relationships through time. Parker et al. (31) use a well-established physiological relationship between turtle body size and temperature to examine trait–environment patterns globally. To do this, they calculate the body sizes of turtle communities from every continent and compare them to anticipated body sizes based on physiological models. They find that globally, the predicted relationship holds for only the largest turtles. However, continentally and through time, patterns do broadly align. Like the papers above, this paper theorizes that anthropogenic land use changes and other biotic impacts may be the cause of observed discrepancies. They emphasize the utility of this method for assessing anthropogenic effects on trait–environment relationships.

Empirically-estimated models of the functional relationship between locomotor strategy and vegetation cover have been useful tools for assessing change in vertebrate functional traits and estimating past vegetation cover. Short et al. (32) evaluate the geographic patterns of ecometric relationships where mismatches occur between locomotor strategies of artiodactyls and carnivorans with vegetation cover. They demonstrate that multitrophic models, including both primary and secondary consumers, better capture trait–environment relationships than calibrated models of either group independently. Applying their multitrophic model to several fossil localities,

they demonstrate the potential of the approach to estimate past vegetation cover and track functional trait change through time. They find that some functional relationships may have been compromised either due to nonrandom extirpation of species or change in vegetation cover.

Identifying a Path Forward

Effective conservation strategies in the midst of rapid change require that we understand past responses to large-scale changes. This special feature demonstrates how one can build models and construct hypotheses relevant to conservation questions that can then be tested using empirical data from long-term experiments and historical and fossil records (Fig. 2). Many of the results described here improve our ecological understanding in a way that can directly inform conservation frameworks. These studies are most effective when they specifically target real, on-the-ground conservation questions.

Knowledge coproduction happens when researchers work with stakeholders to develop research questions and directions most relevant to the needs of the stakeholders (85, 86). This paradigm moves past researchers evaluating what they consider the most relevant problems in their discipline and puts the focus on problems identified by other relevant stakeholders (Fig. 2). In a fully coproduced scientific endeavor, both researchers and stakeholders design research methodology and evaluate and interpret the results (86). Working with stakeholders in knowledge coproduction will help scientists working at longer temporal scales and larger spatial extents produce the kinds of results that conservation organizations need to make prioritization decisions. Even though this approach is time consuming, it may imbue more rapid conservation action from research findings. For example, Wang et al. (33) consulted with The Nature Conservancy to develop a strategy to assess plant range dynamics and climate fidelity, in an effort to align planned research to relevant mission objectives for their resilience and connectivity framework (21).

To make paleontological findings more broadly applicable beyond a single study system, practitioners must be able to access and use the results in pragmatic ways. However, much of the paleontological literature focuses on establishing the significance of historical baselines or purported drivers. These foci fall short of potential contributions of paleontology to conservation, where the most promising contributions result from addressing questions about biotic responses to climate change (55). Kiessling et al. (36) discuss several gaps in the current paleontological literature that could be filled to improve translational science from paleontological findings to decision-making. They point to insufficient reporting of effect size (Table 1; often only *P*-values are reported) and insufficient consideration of scaling effects (Fig. 2). They suggest a roadmap for future research to refine the paleontological contribution to conservation science under a changing climate.

Going forward, integration and translatability will be critical for improving our framework for conserving terrestrial biodiversity. To identify land-purchasing, land-sharing, and other strategies that will allow biodiversity to persist and shift in the face of changing climates, we must know which taxa are most affected by rapidly changing climates and habitat alteration (Fig. 2). To promote and restore functional ecosystems in the midst of these dynamic shifts, we must understand trait–environment relationships and the emergent properties of those relationships that result in a healthy ecosystem (Fig. 3). We must further identify the appropriate partners for establishing these conservation practices and coproduce the knowledge necessary to succeed. Finally, for practitioners to translate these findings into practice, it will be imperative to communicate not only the presence of change but also the magnitude of the effects that result. This will ensure that plant and animal communities maintain sufficient functional trait variety to form new assemblages that will be both connected and resilient under novel conditions.

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