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Authors

Lawler, JJ
Ackerly, DD
Albano, CM
[et al.](#)

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The theory behind, and the challenges of, conserving nature's stage in a time of rapid change

[Joshua J. Lawler](#)

[David D. Ackerly](#)

[Christine M. Albano](#)

[Mark G. Anderson](#)

[Solomon Z. Dobrowski](#)

[Jacquelyn L. Gill](#)

[Nicole E. Heller](#)

[Robert L. Pressey](#)

[Eric W. Sanderson](#)

[Stuart B. Weiss](#)

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Abstract

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Most conservation planning to date has focused on protecting today's biodiversity with the assumption that it will be tomorrow's biodiversity. However, modern climate change has already resulted in distributional shifts of some species and is projected to result in many more shifts in the coming decades. As species redistribute and biotic communities reorganize, conservation plans based on current patterns of biodiversity may fail to adequately protect species in the

future. One approach for addressing this issue is to focus on conserving a range of abiotic conditions in the conservation-planning process. By doing so, it may be possible to conserve an abiotically diverse “stage” upon which evolution will play out and support many actors (biodiversity). We reviewed the fundamental underpinnings of the concept of conserving the abiotic stage, starting with the early observations of von Humboldt, who mapped the concordance of abiotic conditions and vegetation, and progressing to the concept of the ecological niche. We discuss challenges posed by issues of spatial and temporal scale, the role of biotic drivers of species distributions, and latitudinal and topographic variation in relationships between climate and landform. For example, abiotic conditions are not static, but change through time—albeit at different and often relatively slow rates. In some places, biotic interactions play a substantial role in structuring patterns of biodiversity, meaning that patterns of biodiversity may be less tightly linked to the abiotic stage. Furthermore, abiotic drivers of biodiversity can change with latitude and topographic position, meaning that the abiotic stage may need to be defined differently in different places. We conclude that protecting a diversity of abiotic conditions will likely best conserve biodiversity into the future in places where abiotic drivers of species distributions are strong relative to biotic drivers, where the diversity of abiotic settings will be conserved through time, and where connectivity allows for movement among areas providing different abiotic conditions.

Introduction

In the past, as climates changed, many species’ distributions shifted to track suitable conditions. In response to these shifts, plant and animal community composition changed, sometimes resulting in new groupings and ecosystems—including associations with no modern analog (Williams et al. [2001](#)). Current greenhouse-gas concentrations exceed those experienced on earth over the last 800,000 years (IPCC [2013](#)). Species ranges are already changing in ways that are consistent with observed climate change (Pinsky et al. [2013](#)). Forecasts of species range shifts, changes in biota, and novel climates and communities highlight the transient and dynamic nature of the ecosystems and communities that until recently, ecologists and conservation practitioners have treated as relatively static (Svenning & Sandel [2013](#); Heller & Hobbs [2014](#)). Such a realization calls into question the way most systematic broad-scale conservation planning has been done.

To date, most systematic conservation planning has focused on protecting today's biodiversity by prioritizing places that are particularly rich in endemic species (Myers et al. [2000](#)) or sets of areas that collectively represent as many species or ecological systems as possible (Margules & Pressey [2000](#)). Another approach has been to focus on areas of less human influence, so-called wild places or wilderness areas (Sanderson et al. [2002](#)). In nearly every case, however, the current distribution of biota lie at the heart of conservation plans. Large networks of protected areas may capture future species distributions well, despite the large changes that are likely to occur (Hole et al. [2009](#)). Alternatively, current reserves may fail to adequately protect the

biodiversity of a future altered by climate change (Araújo et al. [2004](#); Williams et al. [2012](#)). Thus, studies have begun to try to anticipate projected impacts of climate change on species distributions and to integrate those shifts into the conservation-planning process (e.g., Phillips et al. [2008](#)).

One potentially promising approach to addressing climate change in the conservation-planning process involves selecting areas to protect biodiversity based on the distribution of abiotic conditions (e.g., climate, geology, topography) (Hunter et al. [1988](#); Mackey et al. [1988](#); Kirkpatrick & Brown [1994](#)). Areas that represent a diversity of current abiotic conditions will likely provide the diversity of environments needed to support future biodiversity, even if the climatic conditions and species in those areas change (Ackerly et al. [2010](#); Anderson & Ferree [2010](#); Beier & Brost [2010](#)). Here after, we refer to this approach as conserving nature's stage. Hutchinson provided the metaphors of the “ecological theatre” and the “evolutionary play” (Hutchinson [1965](#)). Here, we merely extend those to include the abiotic stage. Abiotic settings are important both for providing a set of diverse places for today's species to exist and for the on-going evolution of species. The conserving-nature's-stage approach may be applied in two primary ways. First, the conservation of areas with localized abiotic diversity may support a higher number of species and may also allow species to move short distances to track suitable habitat. Second, the conservation of different abiotic settings may ensure that biota adapted to those settings are represented in conservation plans today and in the future. We reviewed ecological observations and theory to provide a foundation for this basic idea of protecting abiotic diversity as a means of protecting biodiversity in a changing climate. We discuss the conditions under which such a strategy will most likely be successful and some of the challenges to applying the strategy in practice.

Abiotic Drivers of Ecological and Evolutionary Patterns and Processes

Early Observations

Although early observations date as far back as the ancient Greeks (Essenwanger [2001](#)), the botanist Karl Ludwig Willdenow was perhaps the first to recognize the dominant role of climate in determining the geography of plants, postulating that vegetation was organized in latitudinal and elevational zones (Willdenow [1805](#)). In the early 19th century, Alexander von Humboldt set out to test Willdenow's theories and was the first to empirically map concordance between vegetation and the abiotic environment in the *Essay on the Geography of Plants*, an exploration of the elevational belts of vegetation on Mount Chimborazo in the Andes (Jackson [2009](#))

(Fig. 1). These initial concepts were formalized into various climate (e.g., Köppen's climate classification [Peel et al. 2007]) and biome (e.g., Holdridge [1947] life zones) classification schemes based on concordant patterns of climate and vegetation.

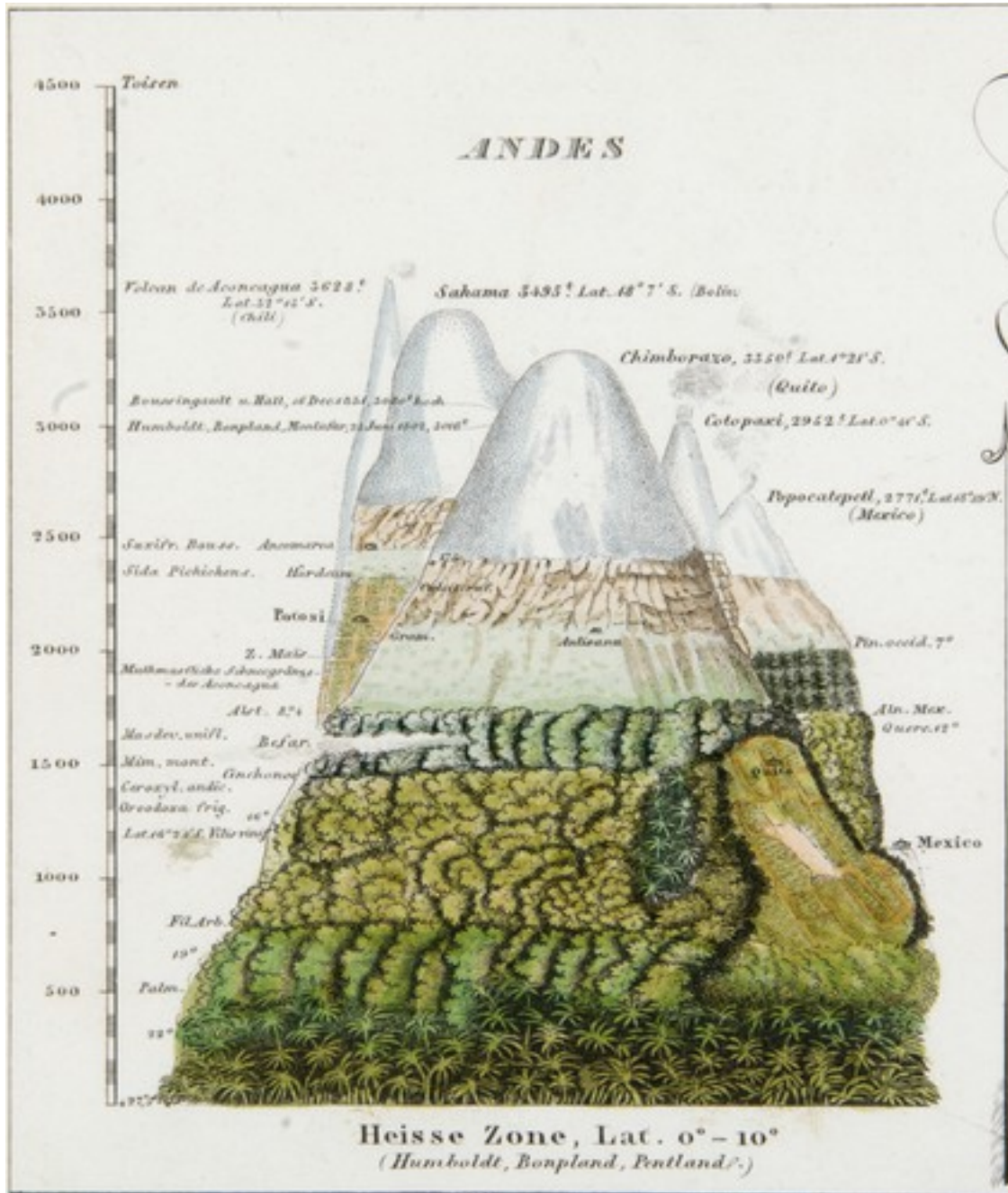


Figure 1
[Open in figure viewerPowerPoint](#)
 Alexander von Humboldt's vegetation of the Andes (source: Anne Buttimer, Alexander von Humboldt and planet Earth's green mantle, Cybergeog : European Journal of Geography [online]. Epistemology, history, teaching document 616. Available

from <http://cybergeogeo.revues.org/25478>, doi:10.4000/cybergeogeo.25478. Online since August 2012 [accessed January 2015]).

Species and Their Environments

Ecologists at the start of the 20th century also focused on the links between the abiotic and the biotic. Clements (1916) developed a theory of vegetation succession that posited that plant communities moved as a unit toward a climax state that depended on environmental conditions like climate, soil, and geology. In contrast, Henry Gleason (1926) saw plants as following individual trajectories with respect to environmental conditions. Paleoecological studies of how plant communities have formed and disassociated with past climatic changes tend to bear out the Gleasonian view (e.g., Brubaker 1989). The contrast between Clements and Gleason about what controls how plant communities change is often seen as a foundational shift in ecological thinking, but underneath the differences, we see consensus about the importance of the abiotic template for shaping the biological responses of organisms (Eliot 2007).

Robert H. Whittaker's work a generation after Clements and Gleason was an effort to map the environmental gradients that shape plant communities (e.g., Whittaker & Niering 1965; Whittaker 1967). Many of the gradients that concerned Whittaker were geophysical, particularly slope, aspect, and soil moisture. He showed that by mapping these gradients and then mapping the distributions of plants, and plant communities, one could infer drivers of community shifts. Austin (e.g., 1977, 1985) furthered understanding of the role of abiotic gradients in structuring plant communities and determining species distributions, leading efforts to statistically link the patterns to their respective drivers.

Animal ecologists too recognized the influence of abiotic factors on species distributions. Grinnell (1917) emphasized the role of the environment—as shaped by climate, landform, and vegetation—in shaping species' geographic ranges and local habitat distributions. Hutchinson (1959) refined these ideas in his semi-quantitative definition of the ecological niche as the set of conditions and resources required for a species to survive; his focus was on local abiotic factors and the distribution of food resources.

Abiotic Drivers of Species Distributions and Patterns of Species Diversity

Since Hutchinson, evidence about how abiotic environments and gradients structure ecological communities has continued to accumulate. Latitude, elevation, geology, soil, and topography all influence climate and the availability of resources, and together they influence species

composition. By 2014 thousands of empirical studies exploring how abiotic factors affect species diversity and species distributions had been published (e.g., Francis & Currie [2003](#); Tittensor et al. [2010](#); Supporting Information for additional citations).

Through its effects on temperature and solar insolation, topography influences water balance and energy availability, which in turn affect abiotic and biotic diversity. For example, steep elevational gradients drive high beta diversity in birds and mammals in the western hemisphere (Melo et al. [2009](#)), and climate and topography are strongly associated with beta diversity of mammals both in North America (Qian et al. [2009](#)) and Europe (Svenning et al. [2011](#)). High beta diversity has also been observed to correspond with fine-scale variation in soils (e.g., Fernandez-Going & Harrison [2013](#)), geology (Anderson & Ferree [2010](#)), and aspect (Gallardo-Cruz et al. [2009](#)) nested within coarser scale climatic, topographic, or elevational gradients.

Geology is an important determinant of the location and diversity of soils, and through soil a determinant of different habitat types (Kruckeberg [2002](#)). Geology shapes species diversity patterns through its influence on the chemical and physical properties of soil and water and by creating topography that redistributes energy and water that results in predictable weather patterns and microclimates. Geology also impacts nutrient availability, pH, and the concentration of toxins, which can, in turn, influence species distributions and the evolution of biota. For example, streams carrying dissolved limestone (CaCO_3) are buffered from decreases in pH resulting from acid deposition and therefore tend to be more hospitable to amphibians with acid-sensitive larva and to mussels that require calcium for basic metabolic function and shell building (Whittier et al. [2008](#)). Calcareous grasslands often support a richer flora and fauna than do acidic grasslands (Harper [1977](#)), although the reverse is true in some acidic grasslands in the southeastern coastal plain of the United States (Noss [2013](#)).

At a very fine, or microscale, abiotic forces interact to define the environmental conditions experienced at a site or by an individual organism. For example, organisms experience the climate near the ground, with all the complexities of the land surface (Geiger et al. [2009](#)). The hierarchical filtering of energy and water fluxes follows deterministic atmospheric processes and environmental biophysics from large-scale weather systems down to the scale of organisms. Elevation lapse rates, associated orographic precipitation, regional and local advection of relatively warm or moist air, insolation loads across aspect and slope, cold air drainage, interactions with plant canopies, evapotranspiration, and the energy balance of organisms themselves all affect microclimates (e.g., Campbell & Norman [1998](#); Geiger et al. [2009](#); Dobrowski [2011](#)), and thus which species are supported in a given place. For example, cushion plants can modify microclimates in alpine environments, moderating substrate temperatures,

increasing soil moisture, and facilitating the establishment of other herbaceous species (Cavieres et al. [2007](#)).

A key nexus between climate and soils is through water-holding capacity, a function of soil depth and texture. Particularly in seasonally arid environments, water-holding capacity defines the balance between actual evapotranspiration and climatic water deficit, which in turn are primary determinants of vegetation composition and physiognomy (Stephenson [1998](#)). At fine spatial scales, variation in water-table depth and soil water-holding capacity can generate heterogeneity in both water deficit and surplus and thus strongly influence plant species distributions in a variety of plant communities (Silvertown et al. [1999](#); Araya et al. [2011](#)). All these examples illustrate that species abundance and compositional types are highly influenced (and predicted) by the interactions of climate, geography, geology, and biota across scales. These factors interact to create a diversity of geophysical types (abiotic settings) that have been used in conservation planning (e.g., Kirkpatrick & Brown [1994](#); Noss et al. [2002](#); Anderson et al. [2015](#) [this issue]).

Topographic and Geologic Diversity and Evolutionary Processes

Topographic diversity influences evolutionary processes in multiple ways. For example, areas of rapid species diversification have been associated with strong elevational or coastal gradients (Cowling & Pressey [2001](#); Davis et al. [2008](#)). Topographic diversity has also influenced the movement of species during past climatic changes. As climates changed in the past, topographic variation, in the form of mountains and valleys and plateaus and basins served as refugia for species (Stewart & Lister [2001](#)). These large areas often harbored climates that were more similar to ones that species had previously experienced either because they generated a diversity of climates or because they were climatically different or decoupled from their surrounding landscape (Ashcroft [2010](#)). Similarly, finer-scale aspects of topography such as swales, hollows, cliffs, hills, and specific aspects may act as microrefugia (Ashcroft [2010](#); Dobrowski [2011](#); Keppel et al. [2012](#)). Isolation and divergence of species within refugia has had significant genetic and evolutionary consequences (Hewitt [2000](#)), and the presence of refugia has been linked to patterns of beta diversity from local (Eriksson [2000](#)) to continental (Svenning et al. [2011](#)) scales. Topographic diversity also strongly influences the velocity of climate change (see following section), which is lower in topographically complex environments. High levels of species richness and endemism have been observed in areas that experienced low climate change velocities during the Quaternary period (Sandel et al. [2011](#)) including the relatively flat terrain of southeastern coastal plain of North America (James [1961](#)), where climatic buffering from the Atlantic and Gulf stream lowered the climate velocities (Grimm et al. [2006](#)).

Geologies and soils also affect the processes of natural selection, speciation, and extinction (Davis et al. [2008](#)). Many species and communities are associated with specific soil types or geologies (Kruckeberg [1986](#); Rajakaruna [2004](#)). For example, 246 serpentine endemics have been documented in the state of California alone (Anacker et al. [2011](#)). Gypsum and limestone soils have also been found to support distinctive plant species and communities (Kruckeberg [2002](#)). Furthermore, the intersections of soil types and elevation zones can be important areas for speciation. These areas provide opportunities for interspecific interactions that can affect evolutionary processes.

Climate Refugia, Topography, and Climate Velocities

Climate refugia—sites that can support isolated populations of species within favorable microclimates during periods of unfavorable regional climate—have been highlighted as potentially useful components of a conservation plan to address climate change (Dobrowski [2011](#); Keppel et al. [2012](#)). It is presumed that in the past, these microrefugia allowed for postglacial colonization via local dispersal (Hampe & Jump [2011](#)). Paleocological evidence for climate refugia is extensive and suggests that a number of taxa requiring relatively warm climates were able to persist during the Pleistocene at higher latitudes than previously appreciated (Stewart & Lister [2001](#); Dobrowski [2011](#)). These findings have spurred interest in understanding if and how climate refugia may promote the long-term maintenance of biodiversity under future climate warming.

A common thread in both the abiotic diversity and the climate refugia literature is the role of landscape heterogeneity in promoting species persistence under changing environmental conditions. Studies exploring fine-grained spatial variability in temperature and moisture in areas of complex terrain suggest that spatial variability in climate may exceed the range of warming expected over the next century (Loarie et al. [2009](#)) and that this variability provides the potential for spatial buffering of climate-change impacts through local dispersal (Scherrer & Körner [2010](#); Lenoir et al. [2013](#)).

Climate-change velocity (Loarie et al. [2009](#)) has been suggested as one metric for use in identifying climate refugia. It is calculated by dividing the rate of climate change through time (e.g., degrees Celsius per year) by the spatial gradient in climate at that location (e.g., degrees Celsius per kilometer). The calculation yields an estimate of the velocity in kilometers per year and direction an organism would need to move to stay within an isocline of a given climate variable. Estimates of climate-change velocity have been derived for temperature and precipitation globally (Loarie et al. [2009](#)) and for the climatic water balance for the conterminous

United States (Dobrowski et al. [2013](#)). Areas with low projected future climate velocities may be more likely to serve as climate refugia than areas with high projected future climate velocities.

Use of Abiotic or Geophysical Settings to Conserve Biodiversity in a Changing Climate

Temporal Scale

One of the principal assumptions made when conserving the abiotic stage is that the geophysical elements that define the stage will remain significantly differentiated as the climate changes. That is, it is assumed that even though the players may change, the existence of multiple abiotic settings will persist. However, no abiotic property is truly stable through time. Rather, like biodiversity, geodiversity is dynamic, changing at rates ranging from short, ecological time scales (years, decades, or centuries) to longer, geological timescales (thousands to millions of years). Moreover, over long time scales, climatic conditions help shape geophysical diversity. That said, the rate of current and predicted warming exceeds that of the Holocene (IPCC [2013](#); Marcott et al. [2013](#)), which is more rapid than many geological processes that influence organisms (Corenblit et al. [2011](#)). Even so, the durability of various abiotic settings will range from centuries to millions of years (Gill et al. [2015](#) [this issue]), which, on the whole, is slower than the ecological and evolutionary processes shaping biodiversity.

Spatial Extent

The scale at which one defines sets of abiotic conditions to be used as targets for conservation planning has the potential to strongly influence the degree to which the conservation of abiotic targets will conserve biodiversity. Perhaps the most important consideration is that some drivers are more important at broad extents and others over relatively small areas (Benton [2009](#)). Whittaker et al. ([2001](#)) proposed a hierarchical framework for discussing the influence of different drivers on patterns of biodiversity (Table [1](#)). At continental to regional extents, climate is often a primary factor influencing the distribution of species (McGill [2010](#)). At regional to landscape extents, soils and topography tend to play stronger roles. At finer extents (landscape to local) the influences of biotic interactions and abiotic or biotic disturbances tend to become increasingly important. Thus, different drivers of heterogeneity may need to be considered when defining abiotic conditions as conservation targets at different scales.

Table 1. Hierarchical schema of drivers of biodiversity at multiple spatial scales modified from Whittaker et al. ([2001](#))*

Spatial scale	Phenomena	Explanatory variables
Local	species richness within local communities or patches	microenvironmental (e.g., microclimates as defined by microtopography and vegetation) and biotic interactions (e.g., grazing)
Landscape	turnover of species between communities or inventory of whole landscape	topography, catena effects, soils, disturbance (e.g., fire)
Regional	differential overlap of species or ranges (e.g., latitudinal gradients)	water-energy dynamics, climate and physiographic modification of same, and residual historical patterns
Inter-regional or continental	replacement of higher taxa (e.g., placental mammals by marsupials)	plate tectonics, major environmental change (catastrophic or otherwise)

- *Biodiversity and its drivers at local, landscape, and regional scales are most pertinent to the majority of conservation-planning activities.

Latitude

The relative importance of different drivers of biodiversity is also likely to vary by latitude. For example, the effects of elevation on species distributions and community composition are particularly strong in the tropics where reduced seasonality leads to stronger effects of elevational gradients in mean temperature (Janzen [1967](#); Ghalambor et al. [2006](#)). Edaphic gradients tend to be strongest in low-latitude, semi-arid regions because water-holding capacity (soil texture and depth) takes on greater importance in driving species patterns as dry season length increases (Balvanera & Aguirre [2006](#)). By contrast, the effect of aspect on climatic conditions is greatest at mid-latitudes (Holland & Steyn [1975](#)).

Topography

Spatial gradients in climate are likely to be relatively stable (e.g., higher elevations will remain cooler than lower elevations) even as overall climatic conditions change. However, the

magnitude and significance of these gradients is likely to shift in some cases. For example, changing macroclimatic and oceanographic conditions may affect wind patterns, the formation of storm fronts, and overall precipitation and temperature. Such macroclimatic changes will, in many cases, affect meso- and topoclimates as they interact with landforms. Shifts in the strength, direction, or moisture content of prevailing winds can dampen the magnitude of orographic and rainshadow effects (Luce et al. [2013](#)). Thus, some gradients that are now important for defining current patterns of species diversity may be less important for defining them in the future, or vice versa.

Strong Biotic Drivers

One assumption of the abiotic stage approach is that as long as a diversity of abiotic settings is preserved, the actors can sort themselves as they will, maintaining overall biodiversity. We know, however, that patterns of biodiversity are not solely a function of abiotic conditions; they are also the result of biotic interactions (Blois et al. [2013](#)), including interactions with people. The actors, or species, in a stage-based conservation approach may themselves play a role as drivers of environmental change, both through the manipulation of the abiotic environment and through strong biotic interactions. Keystone species (Mills et al. [1993](#)), especially ecosystem engineers (Jones et al. [1996](#)) and foundation species (Ellison et al. [2005](#)), may alter the properties of the stage, such as hydrology, soil formation, weathering rates, and even topography (e.g., sand dunes, coastal barriers). Additionally, climate change is expected to lead to spatial and temporal mismatches in species interactions, disrupting specialized or reciprocal interactions and altering the strength of interactions (Lurgi et al. [2012](#)).

The paleoecological record shows that novel associations and biotic interactions can form during intervals of abrupt environmental change (Gill et al. [2009](#); Blois et al. [2013](#)), which may have important impacts on community composition, ecosystem function, and even rates of speciation (Woodburne [2010](#)). On geologic timescales, mass extinctions tend to result in ecological homogenization, producing communities dominated by generalists with broad environmental niches (Chen & Benton [2012](#)). As we enter Earth's sixth mass extinction (Barnosky et al. [2011](#)), biotic interactions may substantially complicate conservation efforts. Even if a diversity of abiotic settings is conserved, the rates of change may be so great and disturbances so widespread that biotic communities will become more homogenized, at least in the near term.

Connectivity

Humans are also a strong driver of species distributions. A sophisticated focus on conservation of abiotic diversity must consider that species will not be able to move through or around human

structures to track suitable locations on the abiotic palette, especially as human activities shift in response to climate change. Conservation efforts will be required to ensure on-going connectivity and to mitigate the effects of human responses to climate change. Creating connectivity between reserves is one of the most-often suggested climate-adaptation strategies (Heller & Zavaleta [2009](#)). Populations linked across climatic gradients are more likely to maintain genetic diversity and to experience in situ adaptation (Sgrò et al. [2011](#)). This is because abiotic diversity is an important source of genetic variation in populations. Gene flow among populations spanning diverse abiotic conditions will increase genetic variability within sites.

Range shifts may occur more easily when there is connectivity across climatic gradients. Populations that can sequentially colonize areas along temperature or rainfall gradients may be better able to keep pace with climate change (e.g., Beier [2012](#)). In topographically complex areas, climatic gradients can be linked across short distances, whereas in flat areas, the distances to link climatic gradients will be greater (Loarie et al. [2009](#)). Brost and Beier ([2012](#)) used least-cost path modeling to design linkages between areas with similar abiotic conditions and across areas with different abiotic conditions and compared the results to linkages designed for focal species. They found that corridors linking areas with similar abiotic conditions performed well for most, though not all, species, whereas focal species corridors did not adequately connect areas with similar abiotic conditions.

How to Use Abiotic Settings in Conservation Planning for Climate Change

If conservation efforts are to succeed in the face of climate change, conservation practitioners will need planning approaches that address how organisms respond to changing conditions. Shakespeare ([1599](#)) gave us the description: “All the world's a stage,/ and all the men and women merely players:/ They have their exits and their entrances;/ And one man in his time plays many parts....” In 1965 G. Evelyn Hutchinson extended this to the metaphor of the ecological theater and the evolutionary play. Plants and animals are the actors in the ecological theater, and indeed climate change will re-sort them by requiring species to move, which will likely lead to the formation of novel communities and ecosystems (sensu Hobbs et al. [2006](#)) (Fig. [2](#)).

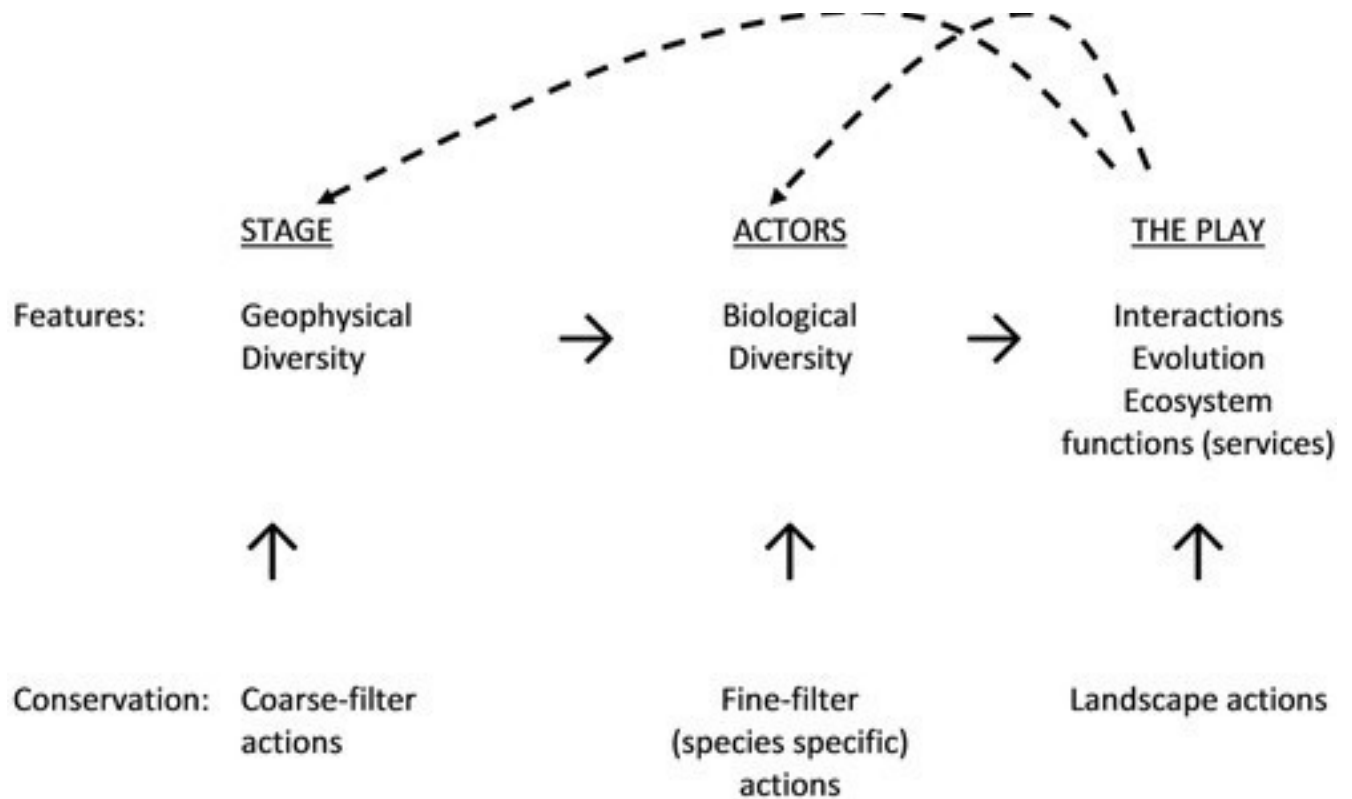


Figure 2

[Open in figure viewerPowerPoint](#)

Conservation of the ecological play (sensu Hutchinson 1959) requires conservation actions directed toward the stage (framed here as geophysical diversity), the actors (i.e., biodiversity), and the play itself, including the interactions among species and between species and the environment. The landscape actions that address the latter must in particular account for issues of size and configuration to engender large enough, dense enough populations with strong interactions, including the actions of species (e.g., ecosystem engineers), that can shape the geophysical stage.

Given what we know about how abiotic diversity drives patterns of biodiversity, it is reasonable to suspect that protecting a diverse abiotic stage will, to some degree, support greater biodiversity today and into the future. Topography, geology, and edaphic conditions will always be part of the ecological stage and will strongly structure the microclimates experienced by species, even as the synoptic-scale climate is changing. The rate of change for most geophysical elements will be slower (relatively speaking) than the capacity of biota to move, which may not be fast enough to keep pace with forecasted climate change in the coming centuries. Therefore, there may be some instances when protecting the stage will work better to conserve biodiversity than species-based approaches.

Although protecting the stage makes intuitive sense as a strategy to address climate change—and is supported by fundamental principles of ecology—there is yet little empirical evidence that

protecting elements of abiotic diversity will result in the protection of future or current biodiversity. Truly testing the former is, of course, impossible. However, it is possible to determine whether areas selected to protect a diversity of abiotic conditions will protect current species, communities, and ecosystems. Results of such tests have been mixed (Beier et al. [2015](#) [this issue]). Furthermore, Schloss et al. ([2011](#)) found that unique combinations of abiotic conditions (abiotic settings) produced spatial patterns that were well aligned with basic vegetation types but that sites selected to most efficiently protect these abiotic setting did a poor job of protecting individual species.

We know that protecting the stage will be more successful where the stage has not been significantly disrupted by anthropogenic activity (Sanderson et al. [2015](#) [this issue]). The degree to which humans have altered the landscape and moved or removed species will affect the success of conserving nature's stage. For example, if a large portion of a region is dominated by urban and agricultural development and infrastructure, conservation plans based on abiotic settings may highlight too many areas in which conservation will be less effective and may easily miss areas with remnant populations of species. This is a limitation of all coarse-filter approaches and is one with which the conservation community is quite familiar.

In addition, conserving nature's stage will likely be a more successful strategy where abiotic drivers play a stronger role than do biotic drivers or historical factors in structuring patterns of biodiversity. In areas where biotic interactions play a large role in determining species distributions, abiotic settings may show little correspondence with patterns of today's biota and may not play a large role in defining future biodiversity. Even in areas where abiotic patterns are the main drivers today, biotic interactions could become more important in the future. For areas where we know that biotic processes have particularly strong impacts on biotic patterns, it may be wise to rely more heavily on alternative approaches to conservation planning that involve modeling climate impacts on species distributions or vegetation patterns or to protect large tracts of land that can provide spatial and temporal refugia from predators and competitors.

Even in places where abiotic drivers of biotic patterns are strong relative to biotic drivers, conserving abiotic diversity alone will not be sufficient for protecting biodiversity in a changing climate. Theory and practice both suggest that conservation of different abiotic settings must always be complemented with conservation efforts that attend to species themselves, particularly species sensitive to human actions and landscape interventions. Humans too will be changing their actions as the climate changes (Watson et al. [2013](#)). The conservation of abiotic diversity is not meant to preclude focal-species conservation efforts, but rather to enhance them.

This, however, raises an important question. If current patterns of biodiversity are closely tied to patterns of abiotic diversity, shouldn't conservation plans designed to protect current biodiversity protect the stage underlying it? This question can be easily addressed. Anderson et al. ([2015](#)) demonstrate how existing conservation plans developed by The Nature Conservancy in the U.S. Pacific Northwestern already account for more than 90% of the abiotic diversity in the region. Thus, specifically adding abiotic settings into the conservation-planning process might not make a dramatic difference in the area required. It may, however, highlight some places that are not necessarily important to species today (e.g., because of extirpations) but that could be important to different species in the future and highlight abiotic settings that are unrepresented in current portfolios (Anderson & Ferree [2010](#)). Furthermore, the use of abiotic settings or diversity to identify potential climate refugia may be an important application of this approach in conservation planning for climate change. Finally, a comprehensive approach to conservation planning will undoubtedly take both abiotic and biotic diversity into account (Kirkpatrick & Brown [1994](#); Noss et al. [2002](#)).

Climate change challenges conservation efforts to ensure the on-going existence of a rich global fauna. The conservation of abiotic diversity, coupled with species conservation efforts, move us to take a broad approach that will hopefully ensure resilience in the face of uncertainty, but this approach does not finish the task. The conservation of biodiversity is not only about the stage or even just the actors, but it is about the play itself (Redford & Feinsinger [2001](#); Soulé et al. [2003](#)). The moon has abiotic diversity, but there is not much call for conservation there. And a zoo, while educating and inspiring us through proximity to mighty actors, is not a place where conservation writ largely happens because a tiger in a cage is not fully a tiger. What the tiger needs, and what we seek to conserve for all species, are interactions with other organisms and their environments (Redford et al. [2011](#)): a stage with many settings and many actors playing many parts.

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