



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

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Abstract: *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.*

Keywords: abiotic factors, climate change, conservation planning, ecological theory

Los Obstáculos y la Teoría detrás de la Conservación del Estado de la Naturaleza en Tiempos de Cambios Rápidos

Resumen: *La mayoría de los planes de conservación a la fecha se han enfocado en proteger a la biodiversidad de hoy bajo la suposición de que será la biodiversidad de mañana. Sin embargo, el cambio climático contemporáneo ya ha resultado en cambios de distribución de algunas especies y se tiene proyectado que resulte en muchos cambios más en las siguientes décadas. Conforme las especies se redistribuyen y las comunidades*

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bióticas se reorganizan, los planes de conservación con base en los patrones actuales de biodiversidad pueden fallar en proteger adecuadamente a las especies en el futuro. Una estrategia para dirigirse a este tema consiste en enfocarse en la conservación de una gama de condiciones abióticas durante el proceso de planeación de la conservación. Al hacer esto, puede ser posible conservar una “etapa” de diversidad abiótica sobre la cual actuará la evolución y sustentará a muchos actores (biodiversidad). Revisamos los apuntes fundamentales del concepto de conservación de la etapa abiótica, comenzando con las observaciones iniciales de von Humboldt, quien mapeó la concordancia de las condiciones abióticas y la vegetación; y progresando hasta el concepto de nicho ecológico. Discutimos los obstáculos impuestos por los temas de escala espacial y temporal, el papel de los conductores bióticos de la distribución de las especies, y la variación latitudinal y topográfica en las relaciones entre el clima y los accidentes geográficos. Por ejemplo, las condiciones abióticas no son estáticas, sino que cambian con el tiempo—no obstante a tasas diferentes y frecuentemente lentas. En algunos lugares, las interacciones bióticas juegan un papel sustancial en los patrones de estructuración de la biodiversidad, lo que significa que los patrones de la biodiversidad pueden estar menos relacionados con la etapa abiótica. Más allá, los conductores abióticos pueden cambiar con la posición topográfica y la latitud, lo que significa que la etapa abiótica necesitará definirse diferentemente en lugares distintos. Concluimos que proteger una diversidad de condiciones abióticas probablemente conserve de mejor manera a la biodiversidad hacia el futuro en lugares donde los conductores abióticos de la distribución de especies son fuertes en relación con los conductores bióticos, donde la diversidad de configuraciones abióticas se mantendrán a lo largo del tiempo, y donde la conectividad permita movimiento entre áreas que proporcionan diferentes condiciones abióticas.

Palabras Clave: cambio climático, condiciones abióticas, planes de conservación, teoría ecológico

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.

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. Paleocological 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

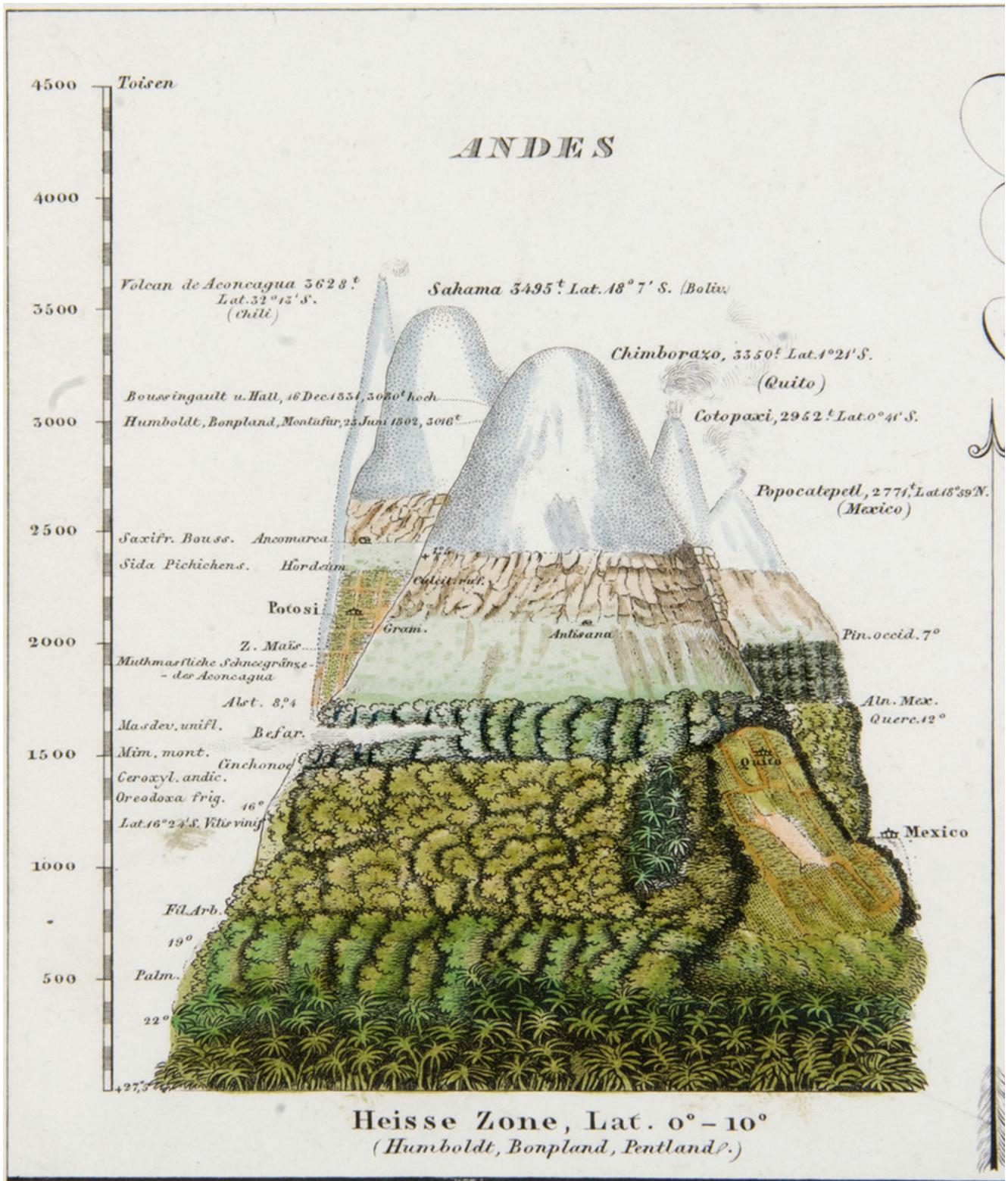


Figure 1. Alexander von Humboldt's vegetation of the Andes (source: Anne Buttner, Alexander von Humboldt and planet Earth's green mantle, Cybergeog : European Journal of Geography [online]. Epistemology, history, teaching document 616. Available from <http://cybergeog.revues.org/25478>, doi:10.4000/cybergeog.25478. Online since August 2012 [accessed January 2015]).

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). Paleoecological 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.

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 topoclimate as they interact with landforms. Shifts in the strength, direction, or moisture content of prevailing winds can dampen the magnitude of orographic and rain-shadow 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.

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

<i>Spatial scale</i>	<i>Phenomena</i>	<i>Explanatory variables</i>
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.

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

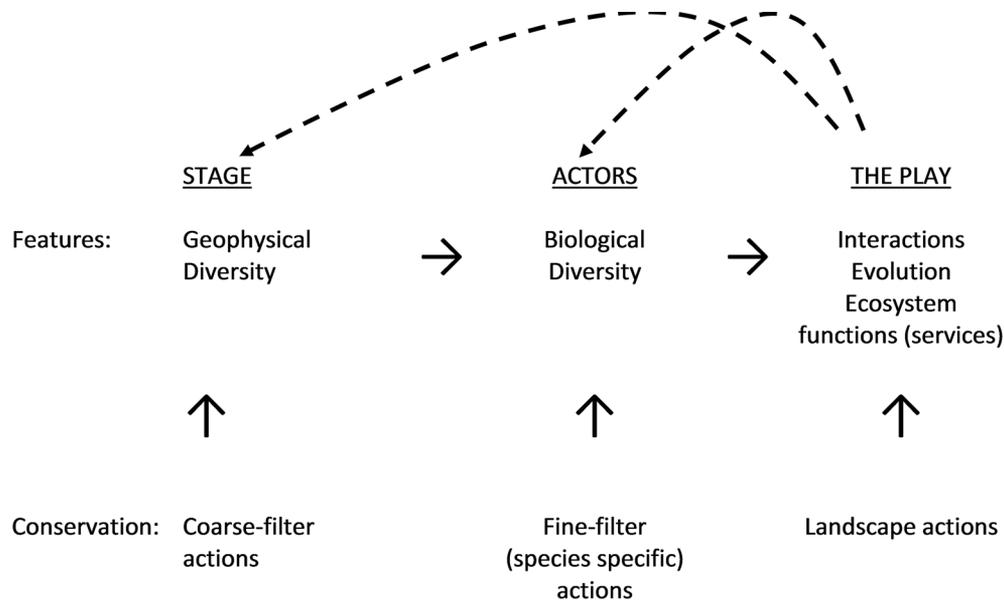


Figure 2. Conservation of the ecological play (sensu Hutchinson 1959) requires conservation actions directed toward the stage (framed here as geophysical diversity), the actors (i.e., biodiversity), and the play itself, including the interactions among species and between species and the environment. 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.

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).

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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Supporting Information

Additional citations on the abiotic drivers of alpha and beta diversity (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

- Ackerly DD, Loarie SR, Cornwell WK, Weiss SB, Hamilton H, Branciforte R, Kraft NJB. 2010. The geography of climate change: implications for conservation biogeography. *Diversity and Distributions* **16**:476-487.
- Anacker BL, Whittall JB, Goldberg EE, Harrison SP. 2011. Origins and consequences of serpentine endemism in the California flora. *Evolution* **65**:365-376.
- Anderson MG, Comer PJ, Beier P, Lawler JJ, Schloss CA, Buttrick S, Albano C, Faith D. 2015. Case studies of conservation plans that incorporated geodiversity. *Conservation Biology* **29**:680-691.
- Anderson MG, Ferree CE. 2010. Conserving the stage: climate change and the geophysical underpinnings of species diversity. *PLOS ONE* **5** (e11554) DOI: 10.1371/journal.pone.0011554.
- Araújo MB, Cabeza M, Thuiller W, Hannah L, Williams PH. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology* **10**:1618-1626.
- Araya YN, Silvertown J, Gowing DJ, McConway KJ, Peter Linder H, Midgley G. 2011. A fundamental, eco-hydrological basis for niche segregation in plant communities. *New Phytologist* **189**:253-258.
- Ashcroft MB. 2010. Identifying refugia from climate change. *Journal of Biogeography* **37**:1407-1413.
- Austin MP. 1977. Use of ordination and other multivariate descriptive methods to study succession. *Vegetatio* **35**:165-175.
- Austin MP. 1985. Continuum concept, ordination methods, and niche theory. *Annual Review of Ecology and Systematics* **16**:39-61.

- Balvanera P, Aguirre E. 2006. Tree diversity, environmental heterogeneity, and productivity in a Mexican tropical dry forest. *Biotropica* **38**:479–491.
- Barnosky AD, et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* **471**:51–57.
- Beier P. 2012. Conceptualizing and designing corridors for climate change. *Ecological Restoration* **30**:312–319.
- Beier P, Brost B. 2010. Use of land facets to plan for climate change: conserving the arenas, not the actors. *Conservation Biology* **24**:701–710.
- Beier P, Sutcliffe P, Hjort J, Faith DP, Pressey RL, Albuquerque F. 2015. Improving the use and evaluation of abiotic surrogates in conservation planning: a review of selection-based surrogacy tests. *Conservation Biology* **29**:668–679.
- Benton MJ. 2009. The red queen and the court jester: species diversity and the role of biotic and abiotic factors through time. *Science* **323**:728–732.
- Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S. 2013. Climate change and the past, present, and future of biotic interactions. *Science* **341**:499–504.
- Brost B, Beier P. 2012. Use of land facets to design linkages for climate change. *Ecological Applications* **22**:87–103.
- Brubaker L. 1989. Vegetation history and anticipating future vegetation change. Pages 41–61 in Agee JK and Johnson DR, editors. *Ecosystem Management for Parks and Wilderness*. University of Washington Press, Seattle.
- Campbell G, Norman JM. 1998. *Introduction to environmental biophysics*. Springer Science and Business, New York.
- Cavieres L, Badano E, Sierra-Almeida A, Molina-Montenegro M. 2007. Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the High Andes of Central Chile. *Arctic, Antarctic, and Alpine Research* **39**:229–236.
- Chen Z-Q, Benton MJ. 2012. The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nature Geoscience* **5**:375–383.
- Clements FE. 1916. *Plant succession: an analysis of the development of vegetation*. Carnegie Institution of Washington, Washington, D.C.
- Corenblit D, Baas ACW, Bornette G, Darrozes J, Delmotte S, Francis RA, Gurnell AM, Julien F, Naiman RJ, Steiger J. 2011. Feedbacks between geomorphology and biota controlling earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth-Science Reviews* **106**:207–331.
- Cowling R, Pressey R. 2001. Rapid plant diversification: planning for an evolutionary future. *Proceedings of the National Academy of Science of the United States of America* **98**:5452–5457.
- Davis EB, Koo MS, Conroy C, Patton JL, Moritz C. 2008. The California Hotspots Project: identifying regions of rapid diversification of mammals. *Molecular ecology* **17**:120–138.
- Dobrowski SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* **17**:1022–1035.
- Dobrowski SZ, Abatzoglou J, Swanson AK, Greenberg JA, Mynsberge AR, Holden ZA, Schwartz MK. 2013. The climate velocity of the contiguous United States during the 20th century. *Global Change Biology* **19**:241–251.
- Eliot C. 2007. Method and metaphysics in Clements's and Gleason's ecological explanations. *Studies in History and Philosophy of Biological and Biomedical Sciences* **38**:85–109.
- Ellison AM, et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* **3**:479–486.
- Eriksson O. 2000. Functional roles of remnant plant populations in communities and ecosystems. *Global Ecology and Biogeography* **9**:443–449.
- Essenwanger OM. 2001. Classification of climates. Page 102 in *World survey of climatology 1C, general climatology*. Elsevier, Amsterdam.
- Fernandez-Going B, Harrison S. 2013. Climate interacts with soil to produce beta diversity in Californian plant communities. *Ecology* **94**:2007–2018.
- Francis AP, Currie DJ. 2003. A globally consistent richness–climate relationship for angiosperms. *The American Naturalist* **161**:523–536.
- Gallardo-Cruz JA, Pérez-García EA, Meave JA. 2009. β -Diversity and vegetation structure as influenced by slope aspect and altitude in a seasonally dry tropical landscape. *Landscape Ecology* **24**:473–482.
- Geiger LE, Aron RH, Todhunter P. 2009. *The climate near the ground*. 7th edition. Rowman & Littlefield Publishing Group, Lanham.
- Ghalambor CK, Huey RB, Martin PR, Tewksbury JJ, Wang G. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology* **46**:5–17.
- Gill JL, Blois JL, Benito B, Dobrowski SZ, Hunter Jr ML, McGuire J. 2015. Conserving the stage for 10,000 years: a paleoecological perspective on coarse-filter strategies. *Conservation Biology* **29**:640–648.
- Gill JL, Williams JW, Jackson ST, Lininger KB, Robinson GS. 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* **326**:1100–1103.
- Gleason HA. 1926. The individualistic concept of the plant association. *Journal of the Torrey Botanical Society* **53**:7–26.
- Grimm EC, Watts WA, Jacobson Jr GL, Hansen BCS, Almquist HR, Dieffenbacher-Krall AC. 2006. Evidence for warm wet Heinrich events in Florida. *Quaternary Science Reviews* **25**:2197–2211.
- Grinnell J. 1917. The niche-relationships of the California Thrasher. *Auk* **34**:427–433.
- Hampe A, Jump AS. 2011. Climate relicts: past, present, future. *Annual Review of Ecology, Evolution, and Systematics* **42**:313–333.
- Harper JL. 1977. *Population biology of plants*. Academic Press, London.
- Heller NE, Hobbs RJ. 2014. Development of a natural practice to adapt conservation goals to global change. *Conservation Biology* **28**:696–704.
- Heller NE, Zavaleta ES. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation* **142**:14–32.
- Hewitt G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* **405**:907–913.
- Hobbs RJ, et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* **15**:1–7.
- Holdridge LR. 1947. Determination of world plant formations from simple climatic data. *Science* **105**:367–368.
- Hole DG, Willis SG, Pain DJ, Fishpool LD, Butchart SHM, Collingham YC, Rahbek C, Huntley B. 2009. Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters* **12**:420–431.
- Holland PG, Steyn DG. 1975. Vegetational responses to latitudinal variations in slope angle and aspect. *Journal of Biogeography* **2**:179.
- Hunter ML, Jacobson GL Jr, Webb T III. 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology* **2**:375–385.
- Hutchinson GE. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? *American Naturalist* **93**:145–159.
- Hutchinson GE. 1965. *The ecological theater and the evolutionary play*. Yale University Press, New Haven, Connecticut.
- IPCC. 2013. *Climate Change 2013: The physical science basis. Contribution of Working Group I to the Fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, New York.

- Jackson ST. 2009. Introduction: Humboldt, ecology, and the cosmos. Pages 1-46 in Jackson ST, editor. *Essay on the geography of plants*. University of Chicago Press, Chicago.
- James CW. 1961. Endemism in Florida. *Brittonia* **13**:225-244.
- Janzen D. 1967. Why mountain passes are higher in the tropics. *The American Naturalist* **101**:223-249.
- Jones CG, Lawton JH, Shachak M. 1996. Organisms as ecosystem engineers. Pages 130-147 in Samson FB, Knopf FL, editors. *Ecosystem management*. Springer, New York.
- Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography* **21**:393-404.
- Kirkpatrick JB, Brown MJ. 1994. A comparison of direct and environmental domain approaches to planning reservation of forest higher plant communities and species in Tasmania. *Conservation Biology* **8**:217-224.
- Kruckeberg A. 1986. An essay: the stimulus of unusual geologies for plant speciation. *Systematic Botany* **11**:455-463.
- Kruckeberg AR. 2002. *Geology and plant life*. University of Washington Press, Seattle.
- Lenoir J, et al. 2013. Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology* **19**:1470-1481.
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009. The velocity of climate change. *Nature* **462**:1052-1055.
- Luce CH, Abatzoglou JT, Holden ZA. 2013. The missing mountain water: slower westerlies decrease orographic enhancement in the Pacific Northwest USA. *Science* **342**:1360-1364.
- Lurgi M, López BC, Montoya JM. 2012. Novel communities from climate change. *Philosophical Transactions of the Royal Society of London B* **367**:2913-2922.
- Mackey BG, Nix HA, Hutchinson MF, Macmahon JP, Fleming PM. 1988. Assessing representativeness of places for conservation reservation and heritage listing. *Environmental Management* **12**:502-514.
- Marcott SA, Shakun JD, Clark PU, Mix AC. 2013. A reconstruction of regional and global temperature for the past 11,300 years. *Science* **339**:1198-1201.
- Margules CR, Pressey RL. 2000. Systematic conservation planning. *Nature* **405**:243-253.
- McGill BJ. 2010. Matters of scale. *Science* **328**:575-576.
- Melo AS, Rangel TFLVB, Diniz-Filho JAF. 2009. Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography* **32**:226-236.
- Mills LS, Soulé ME, Doak DF. 1993. The keystone-species concept in ecology and conservation. *BioScience* **43**:119-224.
- Myers N, Mittermeier RA, Mittermeier CA, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**:853-858.
- Noss RF. 2013. *Forgotten grasslands of the south: natural history and conservation*. Island Press, Washington, D.C.
- Noss RF, Carroll C, Vance-Borland K, Wuerthner G. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. *Conservation Biology* **16**:895-908.
- Peel MC, Finlayson BL, McMahon TA. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* **11**:1633-1644.
- Phillips SJ, Williams P, Midgley G, Archer A. 2008. Optimizing dispersal corridors for the cape proteaceae using network flow. *Ecological Applications* **18**:1200-1211.
- Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. 2013. Marine taxa track local climate velocities. *Science* **341**:1239-1242.
- Qian H, Badgley C, Fox DL. 2009. The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Global Ecology and Biogeography* **18**:111-122.
- Rajakaruna N. 2004. The edaphic factor in the origin of plant species. *International Geology Review* **46**:471-478.
- Redford KH, et al. 2011. What does it mean to successfully conserve a (vertebrate) species? *BioScience* **61**:39-48.
- Redford KH, Feinsinger P. 2001. *The half-empty forest: sustainable use and the ecology of interactions*. Conservation of exploited species. Cambridge University Press, London.
- Sandel B, Arge L, Dalsgaard B, Davies RG, Gaston KJ, Sutherland WJ, Svenning JC. 2011. The influence of Late Quaternary climate-change velocity on species endemism. *Science* **334**:660-664.
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G. 2002. The human footprint and the last of the wild. *BioScience* **52**:891-904.
- Sanderson EW, Segan D, Watson J. 2015. Global geodiversity: How well protected is it? *Conservation Biology* **29**:649-656.
- Scherrer D, Körner C. 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology* **16**:2602-2613.
- Schloss, CA, Lawler JJ, Larson ER, Papendick HL, Case MJ, Evans DM, DeLap JH, Langdon JGR, McRae BH, Hall SA. 2011. Systematic conservation planning in the face of climate change: bet-hedging on the Columbia Plateau. *PLOS ONE* **6** (e28788) DOI: 10.1371/journal.pone.0028788.
- Sgrò CM, Lowe AJ, Hoffmann AA. 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications* **4**:326-337.
- Shakespeare W. 1599. *As you like it*. In Dusinger J, editor. *The Arden Shakespeare*. Bloomsbury, London.
- Silvertown J, Dodd ME, Gowing DJG, Mountford JO. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature* **400**:61-63.
- Soulé ME, Estes JA, Berger J, Del Rio CM. 2003. Ecological effectiveness: conservation goals for interactive species. *Conservation Biology* **17**:1238-1250.
- Stephenson N. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* **25**:855-870.
- Stewart JR, Lister AM. 2001. Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology & Evolution* **16**:608-613.
- Svenning J-C, Fløjgaard C, Baselga A. 2011. Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. *The Journal of Animal Ecology* **80**:393-402.
- Svenning J-C, Sandel B. 2013. Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany* **100**:1266-1286.
- Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, Worm B. 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**:1098-1101.
- Watson JEM, Iwamura T, Butt N. 2013. Mapping vulnerability and conservation adaptation strategies under climate change. *Nature Climate Change* **3**:989-994.
- Whittaker RH. 1967. Gradient analysis of vegetation. *Biological Reviews* **42**:207-264.
- Whittaker RH, Niering WA. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. *Ecology* **46**:429.
- Whittaker RJ, Willis KJ, Field R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* **28**:453-470.
- Whittier TR, Ringold PL, Herlihy AT, Pierson SM. 2008. A calcium-based invasion risk assessment for zebra and quagga mussels

- (*Dreissena* spp). *Frontiers in Ecology and the Environment* 6:180-184.
- Willdenow DC. 1805. *The principles of botany, and of vegetable physiology*. University of Edinburgh Press, Edinburgh.
- Williams J, Shuman B, Webb T. 2001. Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology* 82:3346-3362.
- Williams JW, Kharouba HM, Veloz S, Vellend M, McLachlan J, Liu Z, Otto-Bliesner B, He F. 2012. The ice age ecologist: testing methods for reserve prioritization during the last global warming. *Global Ecology and Biogeography* 22:289-301.
- Woodburne MO. 2010. The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution* 17:245-264.

