

Special Section: Conserving Nature's Stage

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Changing filters

For over 40 years, the U.S. Endangered Species Act (ESA) has, by and large, been an effective tool for fine-filter conservation (i.e., conservation of individual species). But there is a price to pay for the species-by-species approach to conservation. It is easy to trivialize conservation efforts for non-charismatic, oddly named species or to demonize the supposed social callousness of choosing to conserve a lousewort over allowing a hydroelectric project. Moreover, there is a lot of conservation need, and tending to one species at a time in the face of thousands in need promises a long journey to closure. Consequently, conservation professionals have for some time been looking for cogent and practical ways to manage multiple species or systems to strengthen and simplify conservation. Systematic conservation, ecosystem management, and landscape-scale conservation are some of the monikers under which this search has unfolded. The United States is blessed by a plethora of conservation plans (e.g., The Nature Conservancy's ecoregional plans, state wildlife action plans, forthcoming landscape conservation designs) that seek to conserve not only rare species, but also natural community types. The latter plans are meant to capture all the common organisms that never get individual attention. Typically, these plans use native vegetation types as proxies for natural community types, and these vegetation types act as coarse filters to catch the common species. Now, however, the changing climate may force us to change what we use as coarse filter in conservation.

There are many things we do not know about how biodiversity will respond to climate change. One of the few things we do know is that, when climate changes, species respond independently of each other. That is, the natural communities of today will not shift their locations in response to climate change. Rather, their constituent species will rearrange themselves across the landscape as best fits their individual needs. The communities we see and classify and collect in our conservation plans today will disappear and entirely new communities will form. Our existing coarse filter is breaking down. If not for the likely scale of the need, climate change could provide the impetus for a renaissance of single-species management. With perhaps 30% or more of species likely to be stressed by climate change, there could be 12,000 or more species in need of conservation in the United States alone. With that magnitude of conservation need, we will, more than

ever, need a coarse filter for conservation planning, but it should be one that stands up to the challenge of climate change.

I work for the U.S. Fish and Wildlife Service, and one of my major concerns is how to reconcile the recent trend toward higher-level conservation planning (ecoregions, landscapes, etc.) with the independent nature of species adjustments to climate change. No conservation agency I am aware of is currently capable of individualized management for tens of thousands of species. Anderson and Ferree (2010) and Beier and Brost (2010) reminded me of an earlier alternative coarse-filter strategy proposed by Hunter Jr. et al. (1988) to specifically deal with this problem. That alternative was to use the variety of enduring physical features, such as topography, soils, and geology, as a coarse filter to conserve species in a changing climate. The idea being that, to extend G. Evelyn Hutchinson's metaphor of the ecological theater and the evolutionary play, we should focus on conserving the variety of geophysical settings as "stages" for the evolving cast of players sure to be on the move in an era of climate change.

Of course, neither our need for a new filter nor the intuitive appeal of "conserving nature's stage" guarantees this new filter will be effective for the many challenges ahead. So, I was excited to attend an international workshop on the topic, convened by Paul Beier, Mark Anderson, and Malcolm Hunter at the 2013 Society for Conservation Biology meeting, and pleased to see the resulting papers in a *Conservation Biology* special section. The papers in this special section assess the state of the art for this new filter and suggest ways to advance the idea. They remind us of how complicated and nuanced nature is and how frustrating it can be to find clearcut proof of what our instincts tell us must be the right thing to do. The take-home message from the workshop and this collection of papers is that managers can be more confident in large-scale conservation plans that factor in adequate representation of geophysical settings and current biodiversity than in plans that are based solely on current community and species representation.

Conservation has always had a strong foundation in science. In fact, conservation organizations and agencies tout that they are science based or science driven. But the truth is that most agencies and many nongovernmental organizations usually must decide their actions in light

of many unknowns and uncertainties. Our knowledge is never perfect. Professional judgment almost always is the final decider. My advisor in graduate school once told me that the difference between a scientist and a manager is that a scientist is looking for *the* answer and a manager is looking for *an* answer. That is, managers do not necessarily need to know the ultimate truth of a matter as long as they have enough information on which to act that advances the management objective. In this period of profound change, conserving the variety of geophysical settings may be one of the answers to the manager's need for conservation options, even if there is only qualitative evidence that such geodiversity is important to biodiversity. Given the high uncertainty associated with climate change, we may need to place as much, or perhaps more, emphasis on risk-spreading and bet-hedging strategies than on searches for statistical significance.

We are entering a new era of conservation, one where not all the old rules apply. The way forward is unclear and

we need to be creative, flexible, and adaptable. Paying as much attention to what is under all that magnificent green machinery as what is in it may prove a valuable adaptive strategy for conservation.

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Special Section: Conserving Nature's Stage

Life is a gloss on geography. And if you dig your fists into the earth and crumble geography, you strike geology. Climate is the wind of mineral earth's rondure, tilt, and orbit modified by local geological conditions. The Pacific Ocean, the Negev Desert, and the rain forest in Brazil are local geological conditions. So are the slow carp pools and splashing trout riffles of any backyard creek. It is all, God help us, a matter of rocks.

The rocks shape life like hands around swelling dough. In Virginia, the salamanders vary from mountain ridge to mountain ridge, so do the fiddle tunes the old men play. All this because it is hard to move from mountain to mountain. These are not merely anomalous details. This is what life is all about: salamanders, fiddle tunes, you and me and things, the split and burr of it all, the fizz into particulars. No mountains and one salamander, one fiddle tune, would be a lesser world. No continents, no fiddlers. No possum, no soup, no taters. The earth without form is void . . .

Annie Dillard (1982)

Introduction

The papers in this special section address the use of geodiversity as a coarse filter strategy for conserving biodiversity. A coarse filter strategy conserves representative samples of broadly defined environments as a way to conserve most species. However, geodiversity first entered conservation planning for its own sake, not for its ability to support biodiversity. For example, the first national park in the world (Yellowstone [established 1872]), the second national park in the US (Yosemite [1890]), Canada's first national park (Banff [1885]), and New Zealand's first national park (Tongariro [1887]) were each set aside primarily to protect spectacular geophysical features and their associated recreational and cultural values. This history helps explain why some protected area networks do a better job of protecting rocks than biodiversity (Scott et al. 2001).

Although ecologists have long recognized geodiversity as a key driver of biodiversity and species distribution patterns (Lawler et al. 2015), conservation biologists were slow to consider using geodiversity to prioritize areas for biological conservation. In 1982, The Nature Conservancy (TNC) launched the first coarse-filter approach to conservation (TNC 1982; Noss 1987). The TNC approach aimed to conserve examples of each vegetation community, under the assumption that most species would be protected using this filter. Six years later Hunter et al.

(1988) summarized paleoecological evidence that vegetation communities are merely the ephemeral results of recent (often <8,000 years old in temperate zones) range shifts of individual plants species and argued that physical environments would make better surrogates for conservation planning: "we advocate basing the coarse-filter approach on physical environments as arenas of biological activity, rather than on communities, the temporary occupants of those arenas." This apparently was the first time that conserving geodiversity was proposed as a surrogate for conserving biodiversity and thus marks the beginning of conserving nature's stage (CNS).

Although Hunter et al. (1988) specifically proposed CNS as a coarse-filter strategy for conservation in the face of a changing climate, for the ensuing 20 years, when physical environments were used as coarse filters, they were primarily used as surrogates for contemporary biodiversity, not as a climate adaptation strategy (Belbin 1993; Kirkpatrick & Brown 1994; Wessels et al. 1999). A primary motivation was that data on abiotic physical variables were widely available and more consistently mapped than vegetation communities or species distributions. Indeed, CNS was attractive because it could be applied even in areas with no maps of land cover or species distributions.

The next conceptual advance in CNS occurred when Cowling et al. (2003), Rouget et al. (2003, 2006), and Pressey et al. (2007) proposed the use of physical features (e.g., upland-lowland gradients, interfaces between soil types, and sand movement corridors) as surrogates to conserve ecological and evolutionary processes, such as nutrient transport, interspecific interactions, intraspecific genetic diversity (needed for adaptation and speciation), and disturbance regimes (e.g., flooding and mass wasting).

Five years ago, 2 papers revived the idea of CNS as a climate adaptation strategy (Anderson & Ferree 2010; Beier & Brost 2010). Both papers proposed CNS as a coarse-filter alternative to climate-envelope modeling that has emerged as the dominant fine-filter (species by species) strategy for climate adaptation. Climate-envelope models are focused on individual species, and they chain together 5 highly uncertain models: emission scenarios, general circulation models, downscaled circulation models, species-specific climate envelope models, and species-specific range-shift models. The results are used to identify areas that might support persistence and range shifts of each species. Unfortunately, when the models are used responsibly (considering all plausible combinations of scenarios, models, and scales), large

fractions of the landscape are identified as potential high-priority areas (Pearson et al. 2006; Araújo & New 2007). In contrast, CNS is focused on physical places and provides an attractive coarse-filter alternative, identifying areas of expected high climate resilience without complex modeling of climate and individual species' responses.

The CNS approach has gained traction among scientists and practitioners. The Doris Duke Charitable Foundation sponsored a workshop on CNS at ICCB 2013 and has committed US\$31 million to conserve geodiverse lands in the eastern United States. The U.S. Landscape Conservation Cooperative program is assessing the availability of enduring features data in the coterminous USA and evaluating the potential use of geodiversity in planning. After lamenting the fact that many protected area networks over-represented rock and ice, conservation biologists are now asking, "which rocks, what ice, which soil?" (Sanderson et al. 2015). Furthermore, conservation biologists are increasingly investigating other aspects of the physical stage such as how topography modifies climate to create opportunities for species persistence.

Taking Stock of CNS

As proponents of CNS, in 2012 we recognized the need to examine its theoretical basis, its strengths and limitations, and evidence for its utility. In particular, we recognized the need to ground CNS in more than wishful thinking. The fact that conservation biologists desperately need a well-mapped surrogate for species conservation in areas lacking biotic information does not guarantee such surrogates exist. Similarly, aversion to house-of-cards climate envelope models for individual species might make CNS attractive, but it does not prove it is a reliable alternative.

The papers in this special section take stock of CNS as a coarse filter strategy for conservation planning, both for today's biodiversity and in the face of climate change. In these papers, we use the term *geodiversity* to refer to the diversity of conditions defined by geological, geomorphological, and soil features (Gray 2004); the term *abiotic diversity* refers to the union of geophysical diversity and climate diversity, and the term *environmental diversity* refers to combinations of biotic and abiotic factors or as a general term that references any or all of the above-mentioned concepts.

Lawler et al. (2015) provide abundant evidence that geodiversity is a major driver of species distributions and ecological and evolutionary processes in terrestrial systems but that CNS might need to be adapted to particular situations. For example, the influence of geodiversity might be strongest at mid-sized spatial extents (landscape to region), whereas climate might dominate at continental extents and biotic interactions might dominate at local extents. Moreover, edaphic variables may be relatively strong drivers in low-latitude and semi-arid

regions, whereas aspect and insolation may be stronger at mid-latitudes.

Hjort et al. (2015) explain that ecosystems are the product of 3 realms of diversity (geo-, bio-, and climate diversity) and that geodiversity underpins or directly delivers all types of ecosystem services. Thus, although CNS values geodiversity only for its contribution to biodiversity, geodiversity merits protection for its own sake. Hjort et al. also catalog "geosites"—physically unique sites generally smaller than 1 km² that support unique species. Although these sites are unlikely to be identified by multivariate approaches to CNS, practitioners can easily incorporate geosites (many of which are well mapped) into a CNS strategy.

Summarizing evidence from the last 2.6 million years, Gill et al. (2015) report that although past episodes of climate change produced many local extinctions, geodiversity apparently minimized the number of global extinctions caused by climate change. They conclude that CNS "explicitly acknowledges dynamic processes, including extinction, evolution, community turnover, and novelty. That is, it acknowledges change—not necessarily as a hindrance to conservation, but as intrinsic properties of the very nature we aim to conserve."

Sanderson et al. (2015) provide the first global map of land facets (geodiversity types) along with frequency distributions of the sizes of individual facets and then estimate how much of each of the 672 land facet types are in protected status in each of 8 biogeographic realms. Future conservation efforts should focus on the least protected types (low elevation mollisols and vertisols) that are also the most productive for agriculture.

Although most of the papers in the special section have a terrestrial focus, Sutcliffe et al. (2015) demonstrate that tropical marine sites selected to span abiotic surrogates would conserve most species in 11 marine phyla. Abiotic surrogates were especially effective when the variables used to define surrogates were weighted according to their influence on species turnover. Although studies to identify the abiotic drivers of species turnover made such biotically informed surrogates more expensive than surrogates using unweighted variables, the benefits to biodiversity and commercial fisheries justified the cost.

In their review of many tests of how well abiotic diversity (geodiversity and climate diversity combined) represents species, Beier et al. (2015) report that abiotic surrogates represent plant species well and that recently improved abiotic surrogates can greatly improve representation of plants, vertebrates, and marine organisms. This supports the use of abiotic surrogates in areas that lack data on species distributions. If additional tests using purely geophysical surrogates (i.e., excluding climate variables) find similar patterns, this would support use of CNS as a climate adaptation strategy.

In a compendium of 8 case studies that used geodiversity in conservation planning, Anderson et al. (2015)

found that adding geodiversity targets to a traditional conservation plan (i.e., a plan designed to represent vegetation types and species) usually does not increase the total area prioritized or decrease the achievement of other targets. Under these circumstances, using geodiversity surrogates is a low-cost type of bet hedging that results in networks more robust to climate changes but that are compatible and complementary to existing plans.

Comer et al. (2015) describe how geodiversity can be incorporated into the work of agencies with legal, political, and cultural mandates to focus on conservation of particular species. They suggest that a landscape can be classified into 1 of 4 classes of vulnerability to climate change (resistant, resilient, susceptible, and sensitive), depending on the landscape's current geodiversity, ecological intactness, and connectivity. For each class of vulnerability, Comer and colleagues suggest particular activities to manage disturbance, restoration, and connectivity.

Future Development of Conserving Nature's Stage

Conserving nature's stage has earned a place in the climate adaptation toolkit, complementing other approaches such as reducing non-climate stressors, augmenting genetic diversity in restoration plantings, climate envelope modeling, and assisted colonization (Groves et al. 2012; Schmitz et al. 2015). The papers in this special section also support use of CNS as a coarse-filter strategy to conserve species in today's climate in areas lacking data on where species occur. In the next 5 years, we would like to see the following developments related to the use of geodiversity in conservation planning. Our over-riding concern is less with advancing CNS in particular than with providing a strong scientific basis for adaptation strategies that will conserve biodiversity in a changing world.

Increased Use of Geodiversity in Systemic Conservation Planning

Because geodiversity is intended as a surrogate for biodiversity, CNS users are adopting many of the strategies used to set targets for species. Thus Rouget et al. (2003), Beier and Brost (2010), Brost and Beier (2012), Beier (2012), and Anderson et al. (2014, 2015) suggest setting higher targets for rare and distinctive geophysical settings that might support rare species; including large instances of some geophysical settings to support disturbance regimes and large, genetically diverse populations of species associated with that setting; having targets for interspersions of geophysical settings to promote community reassembly, transition to favorable climate during periods of rapid change, and opportunities for evolutionary diversification; and including targets for connectivity and compactness to facilitate range shifts. These provide

a good start on making CNS a practical tool, but there is a lot of room for improvement.

We call attention to 2 understudied aspects of incorporating geodiversity into systematic conservation planning. First, 3 papers in this special section mention the use of geodiversity as a surrogate not only for species, but also for ecological and evolutionary processes. But we lack a theoretical or empirical basis to set quantitative targets to conserve such processes. For years conservation biologists have used the species-area relationships to suggest general guidelines for minimizing species loss. Can we develop similar rules of thumb for the optimum interspersions of geophysical settings or for the minimum proportion of a physical gradient needed to minimize loss of a region's ecosystem services or evolutionary potential? Although the correct rule may not exist, it would be helpful to develop broad sideboards to guide planning. Second, some geophysical settings are expected to be refugia during the coming decades of inevitable climate change, and this function needs to be incorporated into systematic conservation planning. For example, Shoo et al. (2011) noted that 45% of species in Queensland tropical rainforests were restricted to the coolest forest areas and used these relationships to prioritize sites for restoration. The prioritized sites were identified solely from nonclimate variables (elevation, latitude, distance to stream and coast, foliage cover, and solar radiation) and thus such planning fits within a CNS framework.

A More Charismatic Vocabulary

Geodiversity can be charismatic (Fig. 3 in Hjort et al. 2015), but terms like *land facets* and *ecological land units* are technical and sterile. Acceptance of CNS by managers and civil society would probably be advanced if its vocabulary conveyed the idea that the goal is conserving species and life processes. The term *niche* is a good example of a term that originally denoted a physical space, but now connotes multivariate space that is important to life. Might other terms take on similar utility for this new coarse-filter conservation strategy? The term *geodiversity* might be young enough (it was coined about 1993 [Gray 2004:5–6]) to take on a significant life-support flavor. We hope that *conserving nature's stage*, with its allusions to Hutchison's (1965) "ecological theater and the evolutionary play," might resonate with scientists, managers, and civil society and lead to greater appreciation of the link between geodiversity and biodiversity.

Increased Development and Evaluation of Adaptation Strategies

In the first 100 titles produced by Google Scholar for the keywords *climate change biodiversity*, at least 86 papers focused solely on predicting the vulnerability of biodiversity to climate change. No more than 14% of the

papers developed or evaluated an adaptation strategy. This bias toward impact assessment over adaptation is not limited to the academic literature. For example, consider the United States' National Climate Change and Wildlife Science Center, 8 climate science centers, and 22 landscape conservation cooperatives—entities formed since 2009 explicitly to help society take steps to conserve biodiversity in a changing climate. Our perusal of projects listed on the websites of these entities suggests that >90% of their effort focuses on impact assessment and <10% on adaptation strategies such as CNS, climate envelope modeling, assisted colonization, mobile reserves, and enhancement of connectivity.

We advocate a shift of emphasis away from impact assessment and toward development and evaluation of adaptation strategies—including but certainly not limited to CNS. Unfortunately, the most rigorous evaluation of adaptation strategies would be to try various strategies (with replicates and controls) and observe the response of biodiversity over the next 50–100 years. But of course that course of action is too slow and too risky. As an alternative, we advocate a rigorous comparative evaluation of the theoretical foundations, risks, costs, practicality, and likely outcomes of each strategy.

In such comparative evaluations, CNS would probably fare well in terms of practicality and cost. Because it does not depend on a particular future climate (indeed it is hypothesized to work even if climate does not change), it is more likely to be perceived as practical by managers who are skeptical of climate models, or even the very fact of climate change. Because CNS relies heavily on existing protected areas to allow species to shift to new climate space (Beier 2012), it is less expensive than some alternatives. Because it focuses on real places on the landscape, it avoids the open-ended uncertainty of movable reserves or assisted colonization. Because it uses existing, freely available data, CNS avoids delaying conservation action to improve knowledge; priority lands often become unavailable or more expensive during such delays (Grantham et al. 2009).

On nature's stage, the next act has already begun: massive changes to human and natural systems caused by human alteration of the atmosphere. The degree to which the next act is tragic or triumphant depends primarily on how quickly humans reduce concentrations of greenhouse gasses. We hope our modest contributions will help produce adaptation actions that will complement these crucial mitigation actions.

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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*

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 apuntalamientos 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 ecológica

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. Paleoeological 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-Goñi & 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

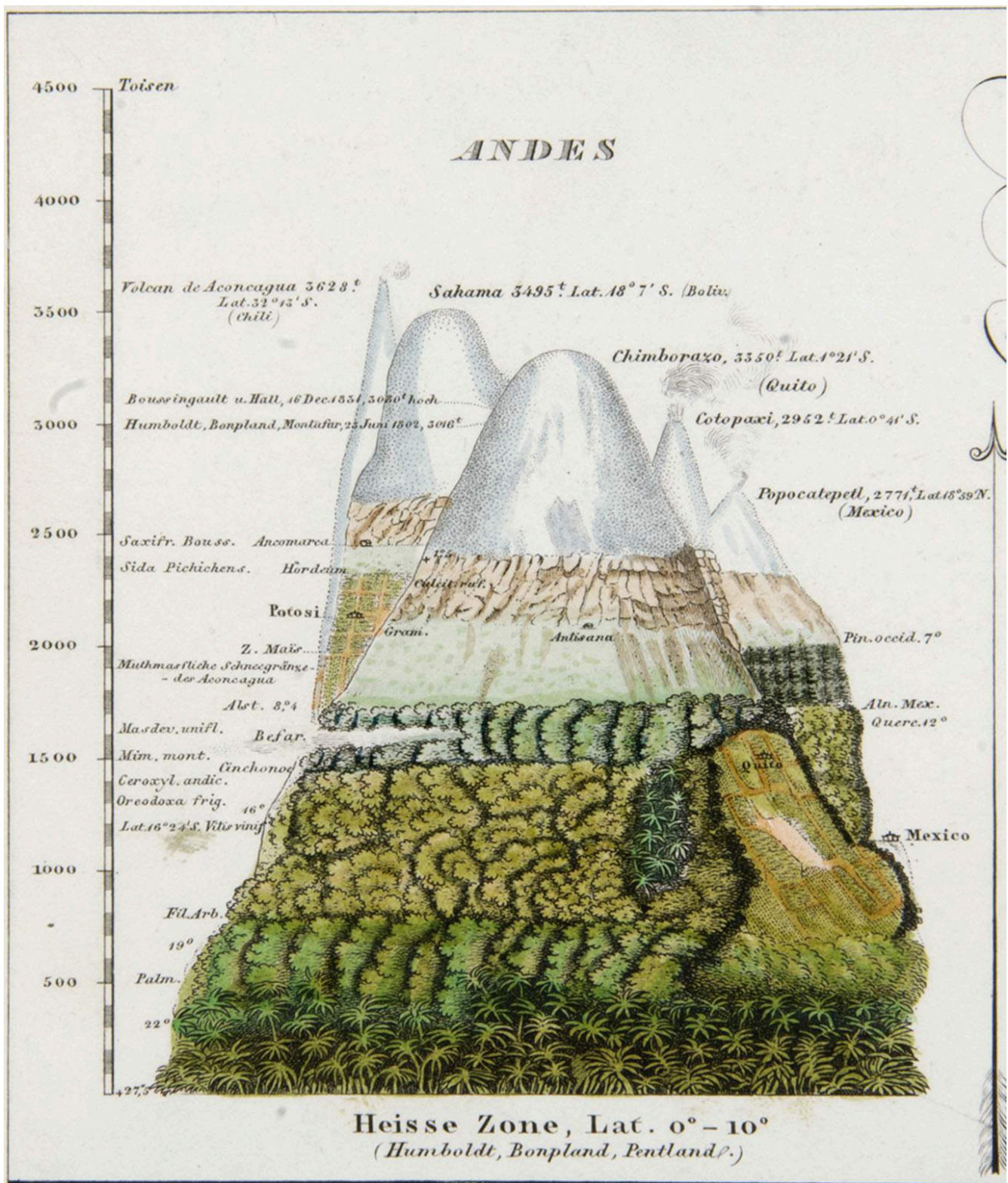


Figure 1. Alexander von Humboldt's vegetation of the Andes (source: Anne Buttner, Alexander von Humboldt and planet Earth's green mantle, Cybergeog : European Journal of Geography [online]. Epistemology, history, teaching document 616. Available from <http://cybergeog.revues.org/25478>, doi:10.4000/cybergeog.25478.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

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 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

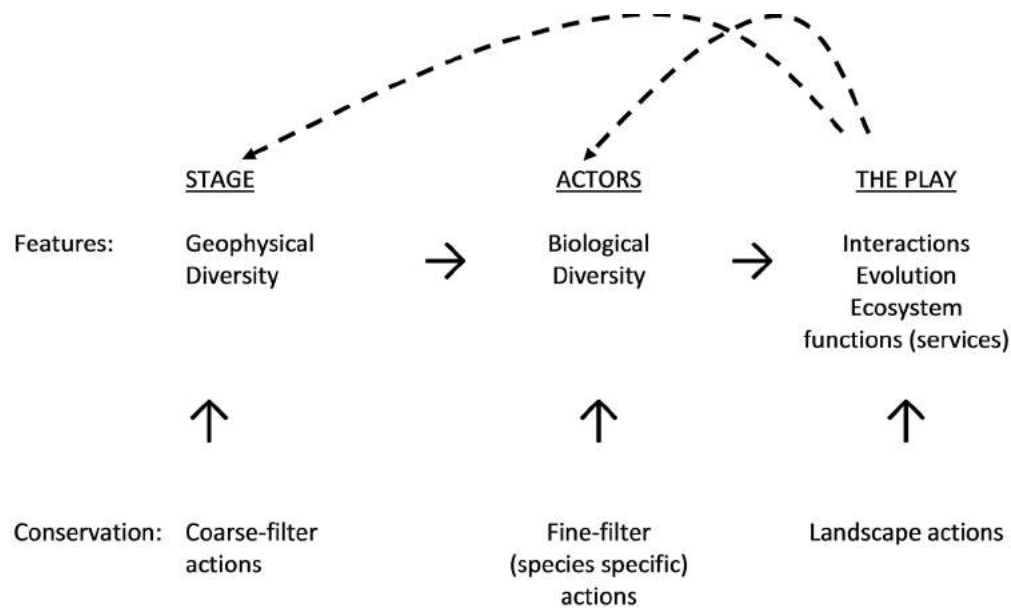


Figure 2. Conservation of the ecological play (sensu Hutchinson 1959) requires conservation actions directed toward the stage (framed here as geophysical diversity), the actors (i.e., biodiversity), and the play itself, including the interactions among species and between species and the environment.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

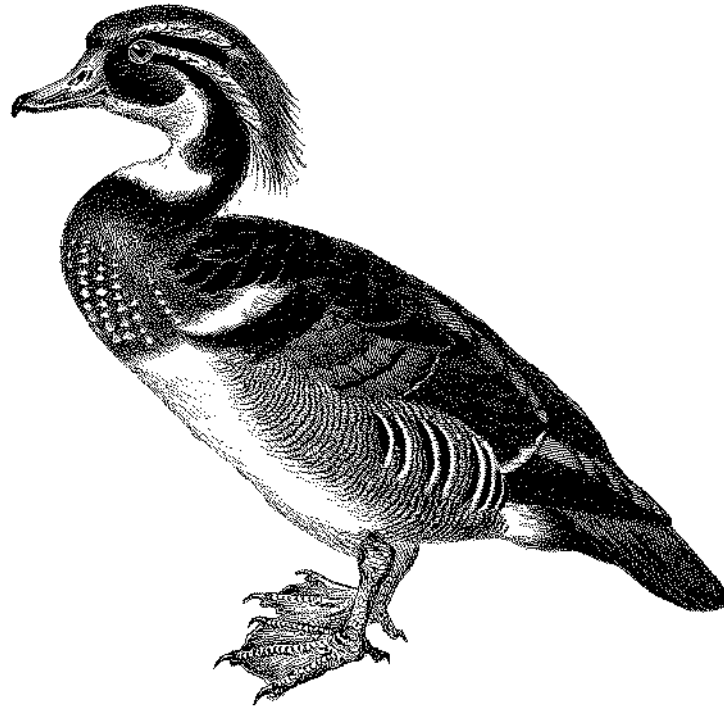
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Lawler et al.: Conserving nature's stage in a time of rapid change: concepts and challenges

Abiotic drivers of individual species distributions and alpha diversity

In addition to the studies cited in the main narrative, other studies documenting associations between abiotic surrogates and species richness (α diversity) include Harner and Harper (1976), Kerr and Packer (1997), Richerson and Lum (1980), Currie & Paquin (1987), Currie (1991), O'Brien (1993, 1998), O'Brien et al. (2000), Francis and Currie (2003), Hawkins et al. (2003a, 2003b), Field et al. (2005), Rangel and Deniz-Filho (2005), Buckley & Jetz (2006), Davies et al. 2007, Kreft and Jetz (2007), Roux et al. (2008), Tittensor et al. (2010), Fitterer et al. (2013), Parks and Mulligan (2010), and Schindler et al. (2013).

Abiotic drivers of beta diversity

In addition to studies described in the main narrative, other studies demonstrating that abiotic variables are associated with species turnover (β diversity) include Guisan and Zimmerman (2000), Carmel and Stoller-Cavari (2006), Bach et al. (2007), Ferrier et al. (2007), Gjerde et al. (2007), Snelder et al. (2007), Buckley and Jetz (2008), Kessler et al. (2009), Padial et al. (2010), Pitcher et al. (2012), Lopez et al. (2011), DiVirgilio et al. (2013), Jones et al. (2013), and Shokri and Gladstone (2013).

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Why geodiversity matters in valuing nature's stage

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Abstract: *Geodiversity—the variability of Earth's surface materials, forms, and physical processes—is an integral part of nature and crucial for sustaining ecosystems and their services. It provides the substrates, landform mosaics, and dynamic physical processes for habitat development and maintenance. By determining the heterogeneity of the physical environment in conjunction with climate interactions, geodiversity has a crucial influence on biodiversity across a wide range of scales. From a literature review, we identified the diverse values of geodiversity; examined examples of the dependencies of biodiversity on geodiversity at a site-specific scale (for geosites <1 km² in area); and evaluated various human-induced threats to geosites and geodiversity. We found that geosites are important to biodiversity because they often support rare or unique biota adapted to distinctive environmental conditions or create a diversity of microenvironments that enhance species richness. Conservation of geodiversity in the face of a range of threats is critical both for effective management of nature's stage and for its own particular values. This requires approaches to nature conservation that integrate climate, biodiversity, and geodiversity at all spatial scales.*

Keywords: abiotic ecosystem services, biodiversity, geosite, cave, hot spring, metalliferous soils, threats to geodiversity

Por Qué Es Importante la Geodiversidad en la Valoración del Estado de la Naturaleza

Resumen: *La geodiversidad—la variabilidad de materiales, formas y procesos físicos de la superficie terrestre—es una parte integral de la naturaleza y es crucial para mantener a los ecosistemas y a sus servicios. Proporciona los sustratos, los mosaicos de accidentes geográficos y los procesos físicos dinámicos para el desarrollo y mantenimiento de los hábitats. Al determinar la heterogeneidad del ambiente físico en conjunto con las interacciones del clima, la geodiversidad ha sido una influencia importante sobre la biodiversidad a través de una gama amplia de escalas. A partir de una revisión bibliográfica, identificamos los valores diversos de la geodiversidad; examinamos ejemplos de las dependencias de la biodiversidad hacia la geodiversidad en una escala específica de sitio (para geositos < 1 Km² de área); y evaluamos varias amenazas inducidas por humanos para los geositos y la geodiversidad. Encontramos que los geositos son importantes para la biodiversidad ya que generalmente mantienen una biota rara o única, la cual está adaptada a condiciones ambientales características o la cual crea una diversidad de microambientes que mejoran la riqueza de especies. La conservación de la geodiversidad de cara a una gama de amenazas es crítica tanto para el manejo efectivo del estado de la naturaleza como para sus propios valores particulares. Esto requiere de enfoques para la conservación de la naturaleza que integran al clima, a la biodiversidad y a la geodiversidad en todas las escalas espaciales.*

Palabras Clave: amenazas para la geodiversidad, biodiversidad, cueva, geositio, manantial, servicios ambientales abióticos, suelos metalíferos

Introduction

The fundamental assumption of the conserving nature's stage approach to maintaining biodiversity is that the physical environment constitutes a stage that will support the actors, the species that are the primary target of biodiversity conservation, even if the actors change due to climate change (Hunter et al. 1988; Anderson & Ferree 2010; Gill et al. 2015; Lawler et al. 2015). This assumption is based on the classic ecosystem concept in which biotic and abiotic components form an interacting system (Tansley 1935). We argue that geodiversity, including small sites that contain particular elements of geodiversity, merits conservation for its own values as well as its importance for biodiversity. First, we considered the diverse values of geodiversity from the perspective of ecosystem services. Second, we examined the interface of biodiversity and geodiversity through the lens of geosites, small geofeatures (< 1 km² in area) that are special environments for biota. The regional scale interface of geodiversity and biodiversity is covered in other articles in this special section (Anderson et al. 2015; Beier et al. 2015; Comer et al. 2015; Sanderson et al. 2015). Finally, we considered various human-induced threats to geosites and geodiversity.

Values of Geodiversity in an Ecosystem Context

Geodiversity is the variability of Earth's surface materials, landforms, and physical processes, for example, materials such as rocks, soils, and water; landforms such as mountains, glaciers, and lakes; and processes such as soil formation, coastal erosion, and sediment transport (Fig. 1) (Gray 2013). Geodiversity is widely recognized for its scientific value and the substantial knowledge benefits it provides for society (e.g., records of past climate changes, the evolution of life, and understanding of how Earth systems operate) (Gray 2013; Gray et al. 2013). However, in the last decade, there has been growing appreciation of the wider values of geodiversity and its links with landscape and biodiversity conservation, economic development, climate change adaptation, sustainable management of land and water, historical and cultural heritage, and people's health and well-being (Table 1) (e.g., Gordon et al. 2012; IUCN 2012; Gray 2013). These values are now embedded within the concept of ecosystem services (Millennium Ecosystem Assessment [MA] 2005). Without the contribution of geodiversity, many of the ecosystem services essential to life on the Earth would not exist or would require vastly expensive technological alternatives (e.g., provision of fresh water, regulation of water and air quality, and soil formation and nutrient cycling for food production). Geodiversity underpins or delivers directly most of the types of ecosystem

services identified in the MA (Fig. 2) (Gray 2011; Gray 2012; Gordon & Barron 2013; Gray et al. 2013). It also provides additional indispensable goods (e.g., minerals, aggregates, and fossil fuels) that are usually considered to be nonrenewable capital assets (Gray 2013).

In the context of conserving nature's stage, geodiversity delivers many essential supporting services for biodiversity including providing the substrate and landform mosaics for the habitat development (static aspect), as well as the soil formation (e.g., Ibáñez et al. 2012; Ibáñez & Bockheim 2013), biogeochemical and water cycling, and geomorphological processes (e.g., water flow regimes, sediment supply, erosion, and deposition) for habitat maintenance (dynamic aspect). To some degree, all ecosystems owe their origins to the geological and geomorphological stage, from entire ocean basins and mountain ranges to small springs and rocky outcrops. As explored throughout this special section, "Conserving Nature's Stage," explicit measures of geodiversity may be among the more useful indicators for the distribution of biodiversity (Pressey et al. 2000; Anderson & Ferree 2010; Beier & Brost 2010; Hjort et al. 2012). For example, Schnitzler et al. (2011) founded a correlation between high geodiversity and biodiversity in a South African biodiversity hotspot. It is also important to emphasize that while many geofeatures such as bedrock geology and topography are stable relative to species distributions (e.g., Beier & Brost 2010), the stage is not simply a static entity and biodiversity is often maintained by dynamic physical processes from micro- to macroscales (Kozłowska et al. 2006; Pressey et al. 2007; Alexandrowicz & Margielewski 2010). For example, some insects rely on processes that continue to create bare soils and sediments on exposed riverine sediments or eroding soft cliffs (O' Callaghan et al. 2013).

Most geomorphological systems are dynamic, with active land-forming processes that differ in magnitude, rate, and location (Thomas 2001). Such complexity across both space and time can be crucial in maintaining biodiversity by determining the heterogeneity of the physical environment (Hunter et al. 1988; Burnett et al. 1998; Nichols et al. 1998). For example, on mountain slopes, the diversity of talus, debris flow, solifluction, frost weathering, snow avalanche, and deflation materials and processes creates mosaics of micro- and mesoscale topography and dynamic environments that support a range of species that would be absent without these processes (e.g., Jonasson et al. 2005; Alexandrowicz & Margielewski 2010). Such dynamic and complex mosaics provide opportunities for high species richness according to the intermediate-disturbance hypothesis (Fox 1981; le Roux & Luoto 2014). They may also help to future-proof ecosystems by conveying a form of spatial and temporal insurance in a changing environment (Tschamntke et al. 2012)

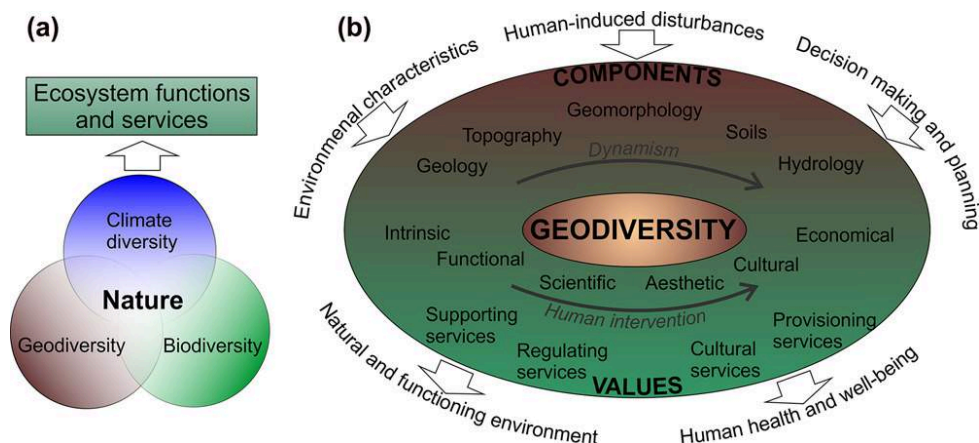


Figure 1. (a) Geodiversity's integral part of nature and importance to ecosystem functions and services (Gray 2011; Beggs 2013). (b) The main components and values of geodiversity and key influences (Gray 2013; Gray et al. 2013).

Table 1. Summary of the principal values and benefits of geodiversity (adapted from Gordon et al. [2012]).

Key values of geodiversity	Geodiversity provides
Maintaining life on Earth	the fundamental materials and hydrological and biogeochemical cycling to enable food and fiber production, provide clean air and water, construction materials, and energy sources
Underpinning biodiversity and landscape	the physical basis or stage (including natural processes) that supports most terrestrial, aquatic, and marine ecosystems and species and the physical basis of the character of valued landscapes (both rural and urban) and seascapes
Economic development	resources and assets for many aspects of economic development, including (geo)tourism-based activities and has a profound influence on the use of land and water
Knowledge of Earth history, materials, and processes	resources for scientific research and education and the knowledge base to help society adapt to climate change and to predict and mitigate natural hazards (including erosion, flooding, and slope failure)
Cultural inspiration	a powerful influence on cultural heritage through inspiration for art, sculpture, music, poetry and literature and on the character of the built environment through the use of different building stones
Recreation and health	a resource for a variety of recreation and outdoor activities and thus benefits for people's health and well-being

and enabling species to adapt or relocate through the availability of suitable environmental mosaics, connections, and elevational opportunities (Brost & Beier 2012).

Geodiversity also harbors information about past biodiversity (fossils, pollen, fungal spores) and about changing factors that affect biodiversity (e.g., climate change, volcanism, erosion, and sedimentation) (cf., Ackerly et al. 2010; Dobrowski 2011; Keppel et al. 2012). Landforms, sediments, and palaeoecological records all document past changes in ecosystems and their development over different timescales (Benton 2009; Hoorn et al. 2010; Schnitzler et al. 2011). While the past is unlikely to provide exact analogues for the future, palaeoenvironmental records have an important part to play in supporting conservation biology, not to provide static baselines or targets, but to inform understanding of ecological and evolutionary processes, ecosystem dynamics, and past ranges of natural variability (envelopes of change) (e.g., Willis & Birks 2006; Dawson et al. 2011; Gill et al. 2015). The long-term (decades to millennia) perspectives provided by palaeoenvironmental records can enable better understanding of trends in ecosystem services (Dearing

et al. 2012; Gray et al. 2013), an acknowledged gap in the MA. For example, both paleo and recent data on river sediment loads can provide insights about the effectiveness of erosion control.

Geosites and Biodiversity Conservation

The interface between geodiversity and biodiversity mainly affects conservation planning at the landscape and regional scales as illustrated in other papers (e.g., Anderson et al. 2015). However, planning at these scales can overlook small geosites (usually <1 km²) that may be very important to biodiversity, perhaps because they harbor a unique biota, such as cave-dwelling species (e.g., Culver & Pipan 2009; Pomory et al. 2011) or metallophytes (e.g., Baker et al. 2004; Whiting et al. 2004). (We also included shores and coasts—even though they are usually measured in linear kilometers—but have provided only a brief treatment here because their importance is already widely recognized in conservation planning and they are readily mapped.) Below and in Supporting Information, we briefly describe 18 types of geosites to

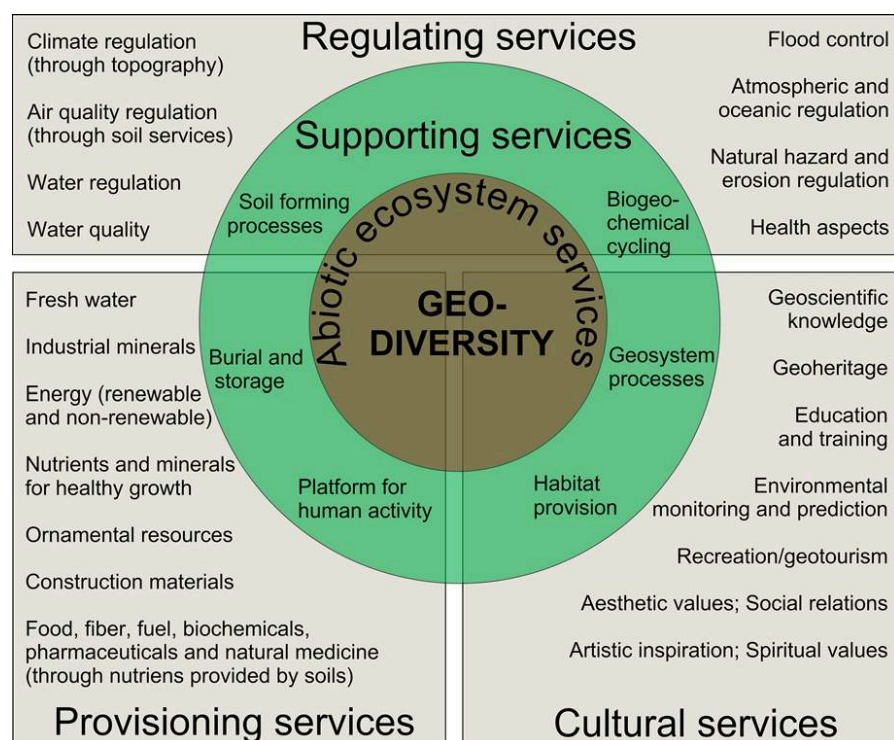


Figure 2. Summary of the ecosystem goods and services provided by geodiversity (Gordon & Barron 2013; Gray et al. 2013).

illustrate the concept. Our list is not exhaustive, but we used it to identify some important examples of geosites (Fig. 3). Moreover, the taxonomy we used is extremely subjective (e.g., all shores are lumped together, but we recognize 3 kinds of spring) but serves our purpose of illuminating the concept.

Caves

Naturally formed underground cavities are one of the clearest examples of why geodiversity is important to biodiversity because they harbor a highly distinctive biota adapted to life in darkness and relatively constant temperature and humidity (Culver & Pipan 2009). Different types of caves often hold a different biota because of variations in geological (e.g., volcanism and karst), hydrological (e.g., fluvial action of subterranean rivers), and biological processes (e.g., production of metabolic heat) (Fig. 3a). For example, anchialine caves contain a mixture of fresh-water and saline water and often have a highly specialized fauna (Pomory et al. 2011). Furthermore, geographic isolation among cave systems can also generate a biota endemic to a limited region. Although cave ecosystems seem separated from the outside environment, they are often highly linked, for example, because of the movement of water or bats. Sometimes millions of bats have an ecological impact for many kilometers around a cave (Culver & Pipan 2009).

Cliffs

Variations in geology (e.g., rock type), size (from small rock outcrops to mountain faces), and aspect (which

generates profound differences in microclimate [cf., Ackerly et al. 2010; Dobrowski 2011]) create distinct cliff habitats for biota that extend into the air above cliffs for aerial species (Larson et al. 2005; Kunz et al. 2008) (Fig. 3b). The dominant but invisible factor driving life on cliffs is gravity. This limits plant life to species that can cling to rocks and soil-filled crevices and animal life to species that can fly or climb very well. For both plants and animals, cliffs offer protection from some predators and competitors and this means some species (e.g., grazing-intolerant plants in areas otherwise subject to extensive grazing by domesticated animals) are usually found only on cliffs (Lambertucci & Ruggiero 2013). Cliffs also allow some species to reach extraordinary densities (e.g., thousands of seabirds nesting on a small cliff face [Larson et al. 2005]).

Limestone Pavements and Alvars

These calcium-rich environments with little or no soil, often due to its removal by glacial erosion, support grassland vegetation with a number of specialized plants, butterflies, ground-nesting birds, and snails. Particularly important are the moist and sheltered habitats in the cracks in limestone pavements (Fröberg et al. 2011) (Fig. 3c). Globally, these geosites are quite rare, mainly but not only limited to small sites in northern Europe and the Great Lakes region of North America.

Metalliferous Soils

These environments (e.g., serpentine and other ultramafic rocks) support metallophytes that are tolerant of

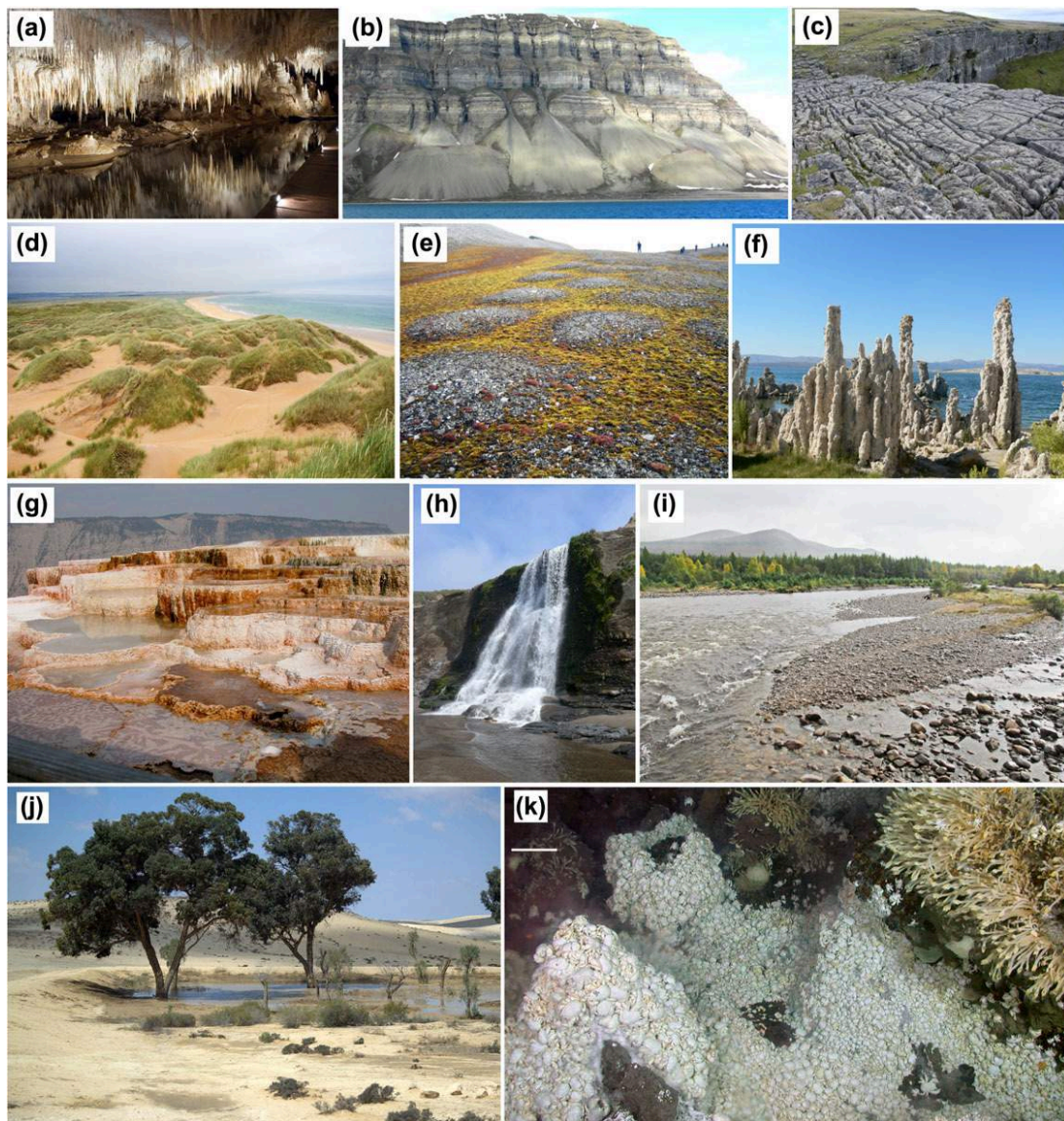


Figure 3. Examples of geosites and small geofeatures (< 1 km² in area) that are special environments for biota (photo credits in parentheses): (a) cave with stalactites and a subterranean stream in Western Australia (Wikimedia Commons, Paul Pickford), (b) cliff and talus cones in Svalbard, Norway (Wikimedia Commons, Wilson44691), (c) limestone pavement, Malham Cove, Yorkshire, United Kingdom (Murray Gray), (d) sand dunes in northeastern Scotland, United Kingdom (John Gordon), (e) patterned ground formed by frost processes on Cobourg Island, Nunavut, Canada (Flickr, Spencer Sweart), (f) tufa towers in Mono Lake, California, United States (Wikimedia Commons, Adrignola), (g) travertine terraces in Yellowstone National Park, United States (Flickr, Ildar Sagdejev), (h) Alamere waterfalls in California, United States (Wikimedia Commons, Renedrivers), (i) gravel river bar in Scotland, United Kingdom (John Gordon), (j) desert spring in the Negev Desert, Israel (Wikimedia Commons, David Shankbone), and (k) deep-sea hydrothermal vent with dense mass of the anomuran crab (*Kiwa n. sp.*) on the East Scotia Ridge, Southern Ocean (scale bar: 10 cm for foreground) (Wikimedia Commons, Papa Lima Whiskey 2).

low calcium:magnesium ratios and high concentrations of heavy metals such as copper, lead, nickel, and zinc (Green et al. 2003; Whiting et al. 2004). In addition to metal-tolerant plants, metalliferous sites may harbor rare bryophytes, lichens, and insects (Baker et al. 2004).

Talus (Scree)

Accumulations of weathered rocks, usually at the base of cliffs, provide cover for a number of species of small mammals, reptiles, amphibians, and invertebrates. Active talus slopes are harsh environments for biota due to

dynamic processes and sometimes microclimate (e.g., cold air circulation) (Růžicka et al. 2012). Instability can limit vegetation to species such as lichens and liverworts or species that can grow in a downward-shifting substrate (Fig. 3b).

Sand Dunes

Wind-driven (i.e., aeolian) sediments present a challenging environment for many plants but some species are able to thrive in these unstable environments and even stabilize them (Packham & Willis 1997) (Fig. 3d). The animal communities of dunes are largely dependent on whatever vegetation can develop (from sparse grass to woodlands), but a number of reptiles and arthropods, notably those that can readily burrow in sand, are confined to these settings (Barrows & Allen 2010).

Frost Sites

Frost- and slope-related periglacial processes generate fine-scale disturbances and microtopographical heterogeneity that shape plant communities (Fig. 3e). In highly active sites, frost processes create novel microhabitats for some plant species thus enhancing species richness of a given site (le Roux & Luoto 2014).

Snow Banks

Deep snow accumulations (i.e., nivation sites) can profoundly affect plant communities by limiting the stress of winter desiccation and cold, and summer droughts, but they also shorten the growing season. Due to the abundant soil moisture, weathering processes are active and produce fine-sediments and nutrients for plants (Björk & Molau 2007). These sites may also act as climate refugia for arctic and alpine species threatened by climate change (e.g., Dobrowski 2011; Keppel et al. 2012).

Temporary Pools

Pools that periodically dry out usually have a profoundly different biota from permanent water bodies (Williams 2006; Calhoun & deMaynadier 2008). This occurs primarily because very few fish species can persist during dry conditions and their absence, as predators and competitors, allows invertebrates and amphibians to flourish. Some plant species also do particularly well in sites that are periodically flooded because they are able to flourish in both the hydrological and the nutrient regime that develops when decomposition alternates between wet and dry. Notably, they are often highly integrated with surrounding ecosystems because of animal migrations (e.g., amphibians that move to pools to breed).

Tufa and Travertine

Calcium carbonate precipitation under relatively cool temperatures (e.g., in streams and lakes) generates tufa (Fig. 3f), whereas travertine is formed in warm or hot waters (e.g., hot springs) (Fig. 3g). They can be habitat for particular species of bryophytes, diatoms, and microbes (Ford & Pedley 1996).

Waterfalls

These are challenging places to live, but some species are able to occupy waterfalls, and thus, avoid competition or predation. In some settings, the high humidity generated by a waterfall is exploited by species living near, but not under, a waterfall (Zilihona & Nummelin 2001) (Fig. 3h).

River Bars

Sediment deposits along rivers are important resting and nesting sites for some birds, crocodilians, and turtles and are habitat for various insects and early successional plants (Fig. 3i). They may be more important when they form isolated islands (Larned et al. 2010).

Springs and Headwater Streams

Although often unknown, unnamed, and underappreciated, these tiny water bodies imbedded in a terrestrial environment can have a disproportionate ecological role because they are primary habitat for some species (e.g., certain insects, amphibians, molluscs, and plants) (Chaves et al. 2008) and are a water source for downstream aquatic ecosystems (Meyer et al. 2007). They are dynamic and diverse environments due to different hydrological (e.g., ephemeral versus perennial), geological (e.g., coarse- versus fine-grained sediments), and chemical (e.g., from alkaline to highly acidic) properties. For example, spring-fed headwaters are characterized by clear water and steady temperatures and flows, whereas rain-induced streams in dry environments are ephemeral with sediment-rich water (Larned et al. 2010).

Desert Springs

Springs in arid environments are particularly important for biodiversity because they are sometimes isolated from other water bodies, which can lead to the evolution of endemic species of fish, snails, crustaceans, and other species (Kodric-Brown & Brown 2007) (Fig. 3j). In some cases, animal populations for many kilometers around a desert spring are dependent on it for water during droughts, and if they are major herbivores this can have wide-ranging effects on vegetation (Valeix 2011).

Table 2. Principal human-induced threats to geodiversity and geosites and examples of impacts (adapted from Gordon & Barron [2011]; Brooks [2013]; Gray [2012]).

<i>Threats</i>	<i>Examples of on-site impacts</i>	<i>Examples of wider impacts on geodiversity</i>
Urbanization, construction (including commercial and industrial developments inland and at the coast, infrastructure) onshore windfarms and related activities	destruction of landforms, fragmentation of site integrity and loss of relationships between features, disruption of geomorphological processes, changes to soil and water regime	contamination of watercourses, changes to geomorphological processes downstream, arising from channelization of water courses or water extraction
Mining and mineral extraction (including extraction from opencast mines, pits, quarries, dunes and beaches, river beds, marine aggregate extraction and deep-sea mining)	destruction of landforms and exposures of sediments and rocks, destruction of soils, soil structure, and soil biota	changes in sediment supply to active process systems leading to enhanced erosion or scour in river and coastal systems, contamination of groundwater
Changes in land use and management (including agriculture, forestry)	landform damage through ploughing, ground leveling and drainage, soil erosion, changes to soil chemistry and soil water regime, soil compaction, loss of organic matter	increase in sediment yield and speed of runoff from catchments, episodic soil erosion leading to increased sedimentation and chemical contamination in rivers, lakes and caves, drying out of wetlands through local and distal drainage
Coastal protection and river management and engineering	damage to landforms and exposures of sediments and rocks, disruption of coastal and fluvial processes, inhibition of erosion allows exposures to become degraded	wider changes to sediment supply and transport, changes in process regime
Offshore activities (including dredging, trawling, renewable energy developments, hydrocarbon exploitation, and waste disposal)	physical damage to landforms and sediments, disruption of underwater physical processes, seabed and sub-seabed surface scour and penetration	changes to sediment movements and hydrodynamic processes
Recreation and geotourism	fragmentation of site integrity, footpath erosion and other localized soil erosion and loss of soil organic matter	
Climate change (especially in terrestrial environments)	changes in active system processes, changes in system state (reactivation or stabilization)	changes in sensitivity of land-forming environments (e.g., rivers, coasts) leading to changes in types and rates of geomorphological processes (e.g., erosion, flooding)
Sea-level rise	loss of visibility and access to coastal exposures and outcrops through submergence, loss of exposures through enhanced erosion	changes in wider patterns of erosion and deposition, enhanced flooding
Restoration of pits and quarries (including landfill)	loss of exposures and natural landforms	
Irresponsible fossil and mineral collecting	physical damage to rock exposures and loss of fossil record	

Hot Springs

Extreme temperatures limit the biota to microorganisms known as thermophiles, but this is a group of great interest to biologists as sources of heat-stable enzymes that are the basis for DNA technology and as models for what may have been the first life forms on Earth or other planets (e.g., Ward et al. 1998).

Shores

Shores and coasts, where the terrestrial, freshwater, and marine realms intersect, are manifestly important to biodiversity, arguably the most important places on the

planet (Gray 1997). Here, many species reach their highest abundances because they are able to access resources from two realms, and many more are uniquely tied to the special conditions of these sites (e.g., the flood and ebb of water [at periodicities ranging from hours to decades, from tides to episodic floods] and the dynamism of substrates generated by erosion and sedimentation). The variability in multiple driving factors means that dozens of kinds of shores can be recognized, each with its own biota. Conservationists are well aware of the importance of shores, and their linear nature makes them generally easy to map for conservation planning (e.g., Gray 1997; Defeo et al. 2009).

Submarine Rock Outcrops

When isolated rock outcrops occur in an expansive bed of marine sediments (e.g., a seagrass bed), they often attract a diverse, abundant biota, most conspicuously fish that are different from species associated with mud or sand flats (e.g., Levinton 2001; McArthur et al. 2010). Thus, they substantially increase the beta diversity of a site. The importance of rock outcrops in marine systems is attested by the popularity of creating artificial reefs to increase fish populations.

Deep-Sea Hydrothermal Vents

These are among the most extreme geofeatures on the Earth. They have steep chemical, pH, and temperature gradients and extremely high pressure, and their complete darkness supports a unique food web based on chemosynthetic bacteria rather than photosynthesis. Diverse invertebrates (most notably tube worms and various crustaceans) depend directly on the bacteria, and various predators are supported too (Fig. 3k). Vents are continuously forming and breaking down through precipitation of minerals, earthquakes, and volcanic eruptions, and this dynamism tends to foster biodiversity because variations in the shape and size of deposits, as well as mineralogy, generate habitat diversity (Van Dover et al. 2002; Boschen et al. 2013).

Threats to Geodiversity

The threats facing geodiversity arise principally from development and land-use changes at both site and wider scales (Table 2) (Prosser et al. 2006; Stace & Larwood 2006; Gordon & Barron 2011; Gray 2013). The principal impacts are physical damage, loss of visibility or access, fragmentation and loss of relationships between features, and interruption of natural processes (e.g., river flow regimes and sediment cycling). Specific geofeatures may be affected by, for example, mineral extraction (e.g., metalliferous sites, limestone pavements), marine dredging, urbanization, agriculture (e.g., springs, temporary pools), bioprospecting (e.g., deep-sea hydrothermal vents, hot springs), and recreational activities (e.g., caves, cliffs, sand dunes) (Gray 2013). Indirect and off-site pressures may also arise from pollutants (e.g., by changing the chemical composition of both surficial and ground waters in caves and lagoons), climate change, and sea-level rise (Table 2) (Prosser et al. 2010).

While some rocks and landforms are relatively robust, degradation and loss of key sites is widespread (Gray 2013). Many features are relict or inactive and, analogous to species extinctions, once damaged or destroyed cannot be replaced. Thus, proactive conservation is essential to ensure the protection of geodiversity for its own direct values (Prosser et al. 2006; Gray 2013) and its interactions

with biodiversity (e.g., Prosser et al. 2011; IUCN 2012). Many countries have introduced legislation to protect geosites, particularly in the developed world, and there is international recognition of geodiversity through, for example, the World Heritage and Global Geopark networks of sites (Global Geoparks Network 2013; Gray 2013; ProGEO 2013).

Conclusions

Geodiversity is crucial for sustaining living species and their habitats, and site-scale conservation targets are often unique due to geodiversity features. Thus, management of sites for biodiversity requires consideration of their geological and geomorphological setting, current state and past history and process dynamics. It is crucial that these aspects of the stage and their links to biodiversity are adequately understood as a basis for developing effective management responses to human pressures and climate change (e.g., Bruneau et al. 2011; Brazier et al. 2012). In many cases, maintaining natural processes will be a key part of conserving biodiversity (e.g., Hopkins et al. 2007; Pressey et al. 2007). Consequently, conservation management of the geodiversity components of the stage is crucial for sustaining species and ecosystems, particularly given the uncertainties about the effects of climate change (e.g., Bellard et al. 2012). At the same time, geodiversity merits conservation for its own considerable values. This requires much more integrated approaches to nature conservation planning and management—both biological and geological—at all scales from small sites to whole landscapes. Geodiversity in general, supported by geoconservation, delivers many fundamental ecosystem services, but this needs to be communicated much more effectively among disciplines, as well as between scientists and decision makers.

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Supporting Information

Examples of types of geosites and small geofeatures that are special environments for biota (Appendix S1) are available online. The authors are solely responsible for the content and functionality of the material. Queries (other than absence of the material) should be directed to the corresponding author.

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Why geodiversity matters in valuing nature's stage

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Appendix S1. Examples of types of geosites, small geofeatures that are special environments for biota.

Types of geosites	Representative taxa	Example species
Cave	bat roost; troglobite arthropods, fishes, salamanders, molluscs	Brazilian free-tailed bat <i>Tadarida brasiliensis</i> Cave glow worm <i>Arachnocampa luminosa</i>
Cliff	raptors & seabird nesting, plants, lichens, insects	Black-legged kittiwake <i>Rissa tridactyla</i> Himalayan cliff honey bee <i>Apis dorsata</i>
Limestone pavement and alvar	plants, snails, butterflies	Narrow-mouthed whorl snail <i>Vertigo angustior</i> Limestone bedstraw <i>Galium sternerii</i>
Metalliferous soils	plants, lichens, butterflies, ants, beetles	Bay Checkerspot <i>Euphydryas editha bayensis</i> Shetland mouse-ear <i>Cerastium nigrescens</i>
Talus (scree)	mammals, reptiles, arthropods, vascular plants, liverworts, lichens	Northern pika <i>Ochotona hyperborea</i> Ice crawler <i>Grylloblatta campodeiformis</i>
Sand dune	lizards, insects, plants	Namib dune gecko <i>Pachydactylus rangei</i> Dune moth <i>Lithariapteryx abroniaella</i>
Frost site	plants, lichens, insects	Glacier buttercup <i>Ranunculus glacialis</i> Mountain stone wetta <i>Hemideina maori</i>
Snow bank	plants, snow fleas, and snow scorpionflies	Snow flea <i>Hypogastrura nivicola</i> Snow rock-moss <i>Andreaea nivalis</i>
Temporary pool	fairy shrimp, seed shrimp, amphibians, insects	Wood frog <i>Lithobates sylvatica</i> Fairy shrimp <i>Chirocephalus diaphanus</i>
Tufa and travertine	bryophytes, diatoms, microbes, caddisfly specialist	Hook-beak tufa-moss <i>Hymenostylium recurvirostrum</i> a caddisfly <i>Rhyacophila pubescens</i>
Waterfall	plants, insects	Waterfall swift <i>Hydrochous gigas</i> Kihansi spray toad <i>Nectophrynoides asperginis</i>
River bar	birds, crocodilians, turtles, plants, insects	Nile crocodile <i>Crocodylus niloticus</i> Sand bar tiger beetle <i>Cicindela columbica</i>
Springs and headwater stream	fishes, insects (e.g., spring-dwelling caddisflies), amphibians, bryophytes	Pygmy sculpin <i>Cottus paulus</i> Mountain Brook Moss <i>Hygrohypnum montanum</i>
Desert spring	fishes, amphibians, wingless insects	Desert pupfish <i>Cyprinodon macularius</i>
Hot spring	bacteria, insects	<i>Thermus aquaticus</i>
Shore	most phyla have many representatives using shores	Shore Plover <i>Thinornis novaeseelandiae</i>
Submarine rock outcrop	fishes	Squarespot rockfish <i>Sebastes hopkinsi</i>
Deep-sea hydrothermal vent	bacteria, archaea, tube worms, snails, shrimps	Giant tube worms <i>Riftia pachyptila</i> Scaly-foot gastropod <i>Crysomallon squamiferum</i>



A 2.5-million-year perspective on coarse-filter strategies for conserving nature's stage

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Abstract: *Climate change will require novel conservation strategies. One such tactic is a coarse-filter approach that focuses on conserving nature's stage (CNS) rather than the actors (individual species). However, there is a temporal mismatch between the long-term goals of conservation and the short-term nature of most ecological studies, which leaves many assumptions untested. Paleoecology provides a valuable perspective on coarse-filter strategies by marshaling the natural experiments of the past to contextualize extinction risk due to the emerging impacts of climate change and anthropogenic threats. We reviewed examples from the paleoecological record that highlight the strengths, opportunities, and caveats of a CNS approach. We focused on the near-time geological past of the Quaternary, during which species were subjected to widespread changes in climate and concomitant changes in the physical environment in general. Species experienced a range of individualistic responses to these changes, including community turnover and novel associations, extinction and speciation, range shifts, changes in local richness and evenness, and both equilibrium and disequilibrium responses. Due to the dynamic nature of species responses to Quaternary climate change, a coarse-filter strategy may be appropriate for many taxa because it can accommodate dynamic processes. However, conservationists should also consider that the persistence of landforms varies across space and time, which could have potential long-term consequences for geodiversity and thus biodiversity.*

Keywords: biodiversity, climate change, conserving nature's stage, geodiversity, geomorphology, land facets, paleoecology, Quaternary

Una Perspectiva de 2.5 Millones de Años de las Estrategias de Filtro Grueso para Conservar el Estado de la Naturaleza

Resumen: *El cambio climático requerirá de estrategias novedosas de conservación. Una de estas tácticas es un enfoque de filtro grueso que se centra en conservar el estado de la naturaleza (CEN) en lugar de los actores (especies individuales). Sin embargo, existe una discordancia temporal entre los objetivos a largo plazo y la naturaleza a corto plazo de la mayoría de los estudios ecológicos, lo que deja muchas suposiciones sin ser comprobadas. La paleo-ecología proporciona una perspectiva valiosa de las estrategias de filtro grueso al reunir a los experimentos naturales del pasado para contextualizar el riesgo de extinción causado por los impactos emergentes del cambio climático y las amenazas antropogénicas. Revisamos la estrategia de CEN desde una perspectiva paleo-ecológica por medio de la examinación de ejemplos del registro paleo-ecológico, los cuales resaltan las fortalezas, oportunidades y advertencias de una estrategia de CEN. Nos enfocamos en el pasado geológico cercano del Cuaternario, durante el cual las especies fueron sujetas a cambios generalizados en el clima y cambios concomitantes en el ambiente físico en general. Las especies experimentaron una gama de respuestas individuales a estos cambios, incluidas respuestas comunitarias y asociaciones novedosas, extinción y especiación, cambios de extensión, cambios en la riqueza y uniformidad local, y respuestas de*

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equilibrio y desequilibrio. Debido a la dinámica natural de la respuesta de las especies al cambio climático del Cuaternario, una estrategia de filtro grueso puede ser adecuada para muchos taxones ya que puede admitir a los procesos dinámicos. Sin embargo, los conservacionistas también deberían considerar que la persistencia de las formas geológicas varía a través del tiempo y el espacio, lo que podría tener consecuencias a largo plazo para la geodiversidad, y por lo tanto para la biodiversidad.

Palabras Clave: biodiversidad, cambio climático, conservación del estado de la naturaleza, Cuaternario, facetas del suelo, geodiversidad, geomorfología, paleo-ecología

Introduction

The dynamic nature of species' distributions complicates the long-term conservation of their habitats. Even with a growing volume of data on species ranges and abundances, tracking and predicting the movements of millions of species over the coming decades are unfeasible (Ficetola et al. 2013). Some have suggested protecting geological diversity as a surrogate for biological diversity (Hunter et al. 1988; Anderson & Ferree 2010; Beier & Brost 2010). Such coarse-filter strategies target large suites of species (Hunter et al. 1988; Hunter 1991), circumventing the challenges of projecting individual species' distributions in the Anthropocene.

The time scale of conservation biology is typically decades at best; thus, many assumptions about longer-term processes remain untested (Willis et al. 2010a; Dietl & Flessa 2011; Conservation Paleobiology Workshop 2012). In contrast, conservation paleobiology uses geohistorical data to investigate phenomena beyond the time scales of human experience (Dietl & Flessa 2011), offering a long-term perspective on biotic responses to global change. Natural experiments in climate change, extinction, species introductions, or other processes may be analogous to the changes facing biodiversity today. The near-time perspective of the Quaternary (the last 2.588 million years) is particularly valuable because it allows a high degree of spatial, temporal, and taxonomic resolution and because the climates, continental positions, geophysical environments, and biota are very similar to their modern counterparts. The 21,000 years since the end of the last ice age capture a particularly rich archive of ecological responses to environmental change. Given this dynamic past, the paleoecological record indicates that a coarse-filter strategy should focus primarily on the stage (i.e., enduring abiotic features of the environment or geodiversity) rather than the ever-changing cast that occupies it (i.e., individual species or communities). A conservation strategy based on geophysical surrogates, or conserving nature's stage (hereafter CNS), is based on ecological principles (Lawler et al. 2015 [this issue]), including a positive relationship between geophysical surrogates and both α and β diversity.

We reviewed the paleoecological evidence in support of CNS, highlighting its strengths, opportunities, and potential caveats. We focused on the Quaternary because it

has many analogs for future environmental change (Dietl & Flessa 2011). Biological responses to Quaternary environmental changes support a conservation approach resilient to species' dynamic ranges, abundances, and interactions. In addition to the long-term perspective on the actors, paleoecology can inform our understanding of the stage; not all so-called enduring features are equally durable, so we also assessed landform resilience at various spatiotemporal scales. Our goal was to highlight opportunities and challenges for a stage-based approach to conservation, illuminated through the lens of the past.

Climate Change and Dynamic Species Responses over 2.5 Million Years

The ice age cycles of the last 2.5 million years provide a useful case study in species responses to global change. These cycles included changes in temperature means, extremes, and seasonality, hydrology, and atmospheric CO₂ concentrations (Petit et al. 1999; Shakun & Carlson 2010; Clark et al. 2012), many of which contributed to no-analog climates (Williams & Jackson 2007). Distributions of ice sheets, permafrost, glacial landforms, and sea levels shifted substantially (Denton et al. 2010). Even our current interglacial has experienced severe, millennia-long droughts and periods of high seasonality (Mayewski et al. 2004). These changes illustrate the ephemeral nature of species' environments, which may change within decades or even years—certainly within the lifespan of many organisms. The abrupt climate change at the beginning of the Holocene 11,700 years ago was analogous to warming predicted for the coming centuries (1.6–6.0 °C per century), providing a useful comparison.

Quaternary biota were surprisingly resilient to global change. There are few documented examples of climate-driven extinctions until the late Pleistocene (Willis et al. 2010b), although such extinctions may have been more prevalent than has been appreciated. Suitable microclimates likely allowed refugial populations to persist in place (Keppel et al. 2012). Species' ability to keep pace with past climate change (Davis 1986; Prentice et al. 1991) suggests a lack of dispersal barriers, one important contrast with today. From a CNS perspective, then, reserve designs should accommodate substantial and

potentially abrupt changes in climate; be sufficiently diverse in microclimates and landscape heterogeneity to allow species to persist in place whenever possible; and lack dispersal barriers. The Quaternary illustrates the range of potential climate changes likely to occur in the future, as well as the fact that changes in one component of the climate system (e.g., CO₂ concentrations) can have concomitant impacts on others (e.g., temperature and sea level). In the following, we briefly review the most substantial biotic changes before discussing how the paleorecord informs CNS approaches.

Individualistic Responses to Climate Change

Species displayed both equilibrium and disequilibrium responses to late Quaternary environmental changes, including community turnover, extinction and speciation, individualistic range shifts, and changes in local richness and evenness (Conservation Paleobiology Workshop 2012). A rich paleobiological record (Brewer et al. 2012) documents a range of past responses to changing environments and demonstrates the challenges of predicting individualistic responses. As temperatures increase in the future, species are expected to move upward in elevation and to higher latitudes (Parmesan 2006; Blois & Hadly 2009). However, fossil observations demonstrate that species' responses were often more complex; species responded individually to climate change, moving in different directions and at different rates (Graham et al. 1996; Jackson & Overpeck 2000; Lyons 2003).

Species distribution models (SDMs) have become a valuable tool in projecting species' future ranges in response to global change, but such models struggle with accuracy when projected into novel climates and are often unable to predict past occurrences in the fossil record (Williams et al. 2012; McGuire & Davis 2013; Varela et al. 2014). SDMs can benefit from improved methods or data (McGuire & Davis 2013), but species' realized niches may shift even over relatively short intervals (Veloz et al. 2012). Efforts to better characterize the fundamental niche by pooling multiple realized niches (Nogués-Bravo 2009) or by tracing niches through time with paleoclimatic proxies and stable isotope geochemistry (Feranec et al. 2007) will allow us to better test niche conservatism and understand rates of evolution in response to environmental change. Predicting individualistic responses to environmental change is further complicated by shifts in species abundances through time. Blois et al. (2010) demonstrated that a weedy generalist became more abundant in northern California at the Pleistocene-Holocene transition. Thus, even if a species does not shift its range as the environment changes, community richness and evenness may alter the character of an ecosystem.

Dispersal and Disequilibrium

Migration and dispersal rates constrain the ability of biota to maintain equilibrium with climate and are thus critical to developing conservation strategies that mitigate climate change impacts. Mean global climate velocity (e.g., climate displacement rates across space) over the next century is estimated at 0.42 km/year for average temperature, with rates varying from 0.08 km/year to 1.26 km/year depending on topography (Loarie et al. 2009) and model resolution (Dobrowski et al. 2012). Species migration rates of this magnitude are unlikely (Thomson et al. 2011; Corlett & Westcott 2013; Svenning & Sandel 2013), suggesting the potential for pronounced migration lags if species fail to keep pace. Moreover, migration lags may be exacerbated by landscape fragmentation and dispersal barriers (Ordóñez et al. 2014). Indeed, several studies have demonstrated a lack of evidence for range shifts in plants due to recent climate change (Bertrand et al. 2011).

In contrast to modern observations, the paleobotanical record has generally supported equilibrium between climate and plant distributions (Davis 1986; Prentice et al. 1991), suggesting that species' dispersal abilities may be greater than those inferred from modern observations. However, recent reviews have questioned this interpretation. First, post-glacial migration rates may not have been as fast as inferred from the pollen record due to the undetected presence of small refugial populations close to the ice margin (Stewart & Lister 2001; Hampe & Jump 2011). Second, multi-century migration lags may be common in the paleobotanical record but are masked by the coarse temporal scale (millennia) of many studies (Svenning & Sandel 2013). Thus, disequilibrium dynamics driven by lagged climate change responses are likely common for sessile species such as plants. If lags between climate shifts and biotic responses are the hallmark of 21st century climate change impacts, these disequilibrium dynamics will present a major challenge to both ecological forecasting and the assessment of conservation strategies.

Ecological Novelty

Novel communities or ecosystems may form in the future as species respond to changes in climate, disturbance, or human activity (Graham 2005; Hobbs 2006; Williams & Jackson 2007) and may present unique challenges to conservation (Seastedt et al. 2008; Hobbs et al. 2009). In the North American paleorecord, novel plant associations are well documented during the Pleistocene-Holocene transition (16,000–11,000 BP; Jackson & Williams 2004). These no-analog pollen assemblages likely resulted from the combination of novel climates combined with release from herbivory following the end-Pleistocene megafaunal extinctions (Gill et al. 2009; Gill et al. 2012).

Similarly, species' individualistic responses to deglacial climatic change drove the formation of no-analog mammal associations (Graham 2005). The Quaternary paleobiological record thus illustrates the fragility of communities as conservation units and the importance of extrinsic, abiotic factors in driving community assembly (Meachen & Roberts 2014).

Evolution

The CNS approach is intended to preserve evolutionary processes that promote biodiversity, and the genetic and macro-evolutionary responses recorded in the paleorecord provide valuable evidence for whether this strategy may be successful. Environmental variation may contribute to speciation by fragmenting populations and restricting gene flow, allowing populations to follow independent evolutionary trajectories (Endler 1977; Coyne 1992; Doebeli & Dieckmann 2003; Carstens & Knowles 2007). Given the strong climatic, vegetation, and edaphic changes that occurred across the glacial-interglacial cycles, there should be strong links between Quaternary climate change and speciation. Speciation trends have been variable across taxa and environments through the Quaternary, however. Some taxa, such as warblers (Johnson & Cicero 2004) and Mediterranean flora (Coleman et al. 2003), underwent radiations. Others, such as some European alpine plants (Kadereit et al. 2004), experienced reduced speciation rates and still other taxa showed no differences in speciation rates, including North American mammals (Alroy 2000; Barnosky 2005) and plants (Willis & Niklas 2004). For many taxa, however, significant population divergence and changes in genetic diversity have occurred across the Quaternary (e.g., Arbogast 1999; Knowles 2001; Baker et al. 2005; Dalén et al. 2007; O'Keefe et al. 2009; Brace et al. 2012), which indicates that 2.5 million years may not be enough time to generate appreciable speciation for most taxa, though it may portend future speciation. Additionally, the Quaternary glacial-interglacial cycles may have selected for species that are resilient to climate change (e.g., Lister 2004). Future climatic and environmental changes will likely have similar, if not more pronounced, effects. Regardless of whether one focuses on population divergence or on climate resilience, the underlying ecological and evolutionary processes should be preserved.

Links between genetic diversity and geographic and landscape structure have been long recognized (Manel et al. 2003). One of the most important ways that the geophysical setting can provide insights into genetic diversity is through the identification of past and future refugia (Keppel et al. 2012). Mountains have been important refuges because they provide diverse microclimates and environmental heterogeneity (Dobrowski 2011; Ford et al. 2013). Additionally, climate velocity is lower in

mountains because altitudinal shifts tend to be shorter than latitudinal movements to track climates (Loarie et al. 2009). However, it can be difficult to link genetic diversity and evolutionary history beyond the past 100,000 years (Hewitt 2001), inhibiting inference of how well CNS will preserve long-term evolutionary processes.

Extinction

Extinction and extirpation in the Quaternary were the result of interactions between long-term climate and geophysical changes, as well as short-term changes in climate and human activity. Reserve designs would ideally accommodate all these processes to maximize enduring features (e.g., regions minimally influenced by sea level changes or land use). Despite repeated and rapid Quaternary climate change, extinction appears to be quite rare (Willis et al. 2010b), and the recent fossil record is largely one of resilience and adaptation. One notable exception is the end-Pleistocene megafaunal extinction, which highlights the vulnerability of species to interactions between climate change and human activity (Lorenzen et al. 2011). The functional loss of keystone herbivores had major impacts on biota at both local and regional scales, causing community change and novel associations and altering ecosystem functions such as fire, nutrient cycling, and dispersal (Gill et al. 2009; Johnson 2009; Rule et al. 2012; Gill 2014). Local extirpations of small mammals greatly influenced species-level genetic diversity (O'Keefe et al. 2009; Brace et al. 2012). Known climate-driven extinctions appear to be associated with a diverse range of mechanisms, including rapid climate change (Barnosky & Lindsey 2010), regime shifts (Svenning 2003), and habitat loss (Nogués-Bravo et al. 2008). Changes in the sea level (Emslie 1998; Murray-Wallace & Woodroffe 2014) and moisture were important mechanisms for driving extinction, particularly when coupled with dispersal barriers (Sondaar & Van der Geer 2005). While extinction occurred only within a few small mammals at the end of the Pleistocene (Stuart 1991; Koch & Barnosky 2006), regional extirpations were widespread (Grayson 2005; Carrasco et al. 2009; Brace et al. 2012). Further work is needed to constrain climate-driven extinctions throughout the Quaternary and may shed light on the mechanisms most important in driving future biodiversity losses (J.L.G. and D.F. Sax, unpublished).

Endurance of Nature's Stage

The Quaternary paleorecord demonstrates that many aspects of biodiversity are transient through time, undermining static, species-specific approaches to conservation. This perspective supports a CNS approach focused on capturing the physical structures underlying biotic processes. However, we ask: How enduring are

the features chosen to provide a foundation for future biodiversity? Characterizing the dynamic nature of many landforms—across both space and time—is essential to assessing the biodiversity-geodiversity linkage through time, as well as the feasibility of CNS on evolutionary time scales.

The geologic record provides evidence of the formation, movement, and dissolution of landforms over millions of years or more. To assess stability of the stage, evidence of a past landform must be identified as well as dated, either in absolute or relative terms. This is most feasible for landforms that leave a clear sedimentary signature, such as buried soils, loess (dust) deposits, sand dunes, glacial landforms, river terraces, beaches, or oxbows lakes. Dating becomes more complicated for older periods in the geologic record, and error margins increase with time. Despite these limitations, the geologic and paleoecologic records provide useful evidence of both landform evolution and biodiversity change through time, making up for spatiotemporal or taxonomic precision with an immense breadth (Dietl & Flessa 2011). We highlight a few examples that illustrate the dynamic nature of landforms across space and time.

In the short term (years to decades), human activity is one of the most important factors influencing the durability of physiographic units (Steffen et al. 2007). For example, the Aral Sea was once the fourth largest lake in the world (Micklin 2007), but irrigation has reduced it to a tenth of its historic distribution. The sea's desiccation and salinization have created an ecological and economic disaster: the end of commercial fisheries, extinction of the Aral salmon, extirpation of 30 bird species, and extensive damages to tributaries (Severskiy et al. 2005). Natural processes can also severely influence or even eliminate entire ecosystems over short periods. Deltas change dramatically depending on the complex interactions of sea level, sedimentation (influenced by climate or human activity), river discharge, and position (Zong et al. 2012). Salt marshes are sensitive to the magnitude, frequency, and duration of tidal inundation, which is in turn affected by the sea level (Donnelly & Bertness 2001), flooding, tsunamis, or storms (Goodbred et al. 1998; Cochran et al. 2005). Major storm surges indicated by records of paleotempests have been relatively common; at least seven were found (four from Category 5 hurricanes) in a 700-year sediment record from Rhode Island, U.S.A. (Donnelly et al. 2001).

Landforms also evolve on longer time scales (decades to eons). The activation and migration of sand dunes in the North American midcontinent during the Mid-Holocene occurred during decade-to-century-scale droughts that exceeded historical conditions (Forman et al. 2001); the most recent of these ended only 700 years ago (Miao et al. 2006; Mason et al. 2011). The Sonoran piedmonts exhibited episodic and discontinuous periods of aggradation and erosion that took place over

millennia, which increased soil heterogeneity, landform age, and associated vegetation. In this case, species diversity was highest on the most unstable erosional slopes (McAuliffe 1994). Even extremely slow processes, such as lake sedimentation, demonstrate that land facets may only be durable over centennial or millennial time scales (Goring et al. 2012). An extreme example is the megalake Chad. During the late Quaternary, the lake occupied the largest closed basin in the world, its paleolake shoreline was 3100 km, and it covered an area of 340,000 km². Since that time it has been significantly reduced by severe drought, including events at 7700 and 5500 years ago, and a minor filling event between 3700 and 3000 years ago (Leblanc et al. 2006).

Glacial landforms may be at particular risk because they are modified by natural and anthropogenic processes but are unlikely to be replaced without future glaciations. Many sedimentary glacial landforms (e.g., eskers and drumlins) are actively quarried. Even in the absence of human activity, the degradation of steep landforms can occur on the order of centuries (Putkonen & O'Neal 2006). These features not only have intrinsic and scientific values (Dietl & Flessa 2011), but their loss also represents a long-term homogenization of the biotic stage.

Overall, geodiversity itself is dynamic, particularly when global change or anthropogenic impacts are considered. Furthermore, most ecological studies operate on a very small spatiotemporal scale relative to landform stability, which may convey a false sense of durability. Policy makers and conservation planners must thus consider the durability of ecological arenas, define which physiographic units are suitable for long-term conservation planning, and decide which of them (e.g., coastal and riverine environments) should be actively managed due to their low durability across both space and time (Fig. 1). A CNS framework does not presuppose a static environment, but given the relationship between geodiversity and biodiversity, the long-term preservation of geomorphic heterogeneity is a critical component of any CNS-based management plan.

Conclusions

Paleoecology offers an opportunity to test the long-term suitability of CNS, though explicitly linking biodiversity patterns with past geophysical properties can be challenging. Integrating geomorphology, geology, and paleoecology can provide a foundation for understanding links between ecological and landscape diversity across temporal scales. In the meantime, climate dissimilarity, climate velocity, and climate stability (Williams & Jackson 2007; Loarie et al. 2009; Iwamura et al. 2010; Nogués-Bravo et al. 2010; Ashcroft et al. 2012) are more readily extracted from the paleorecord than records of geomorphologic change, are available at broader spatial and temporal

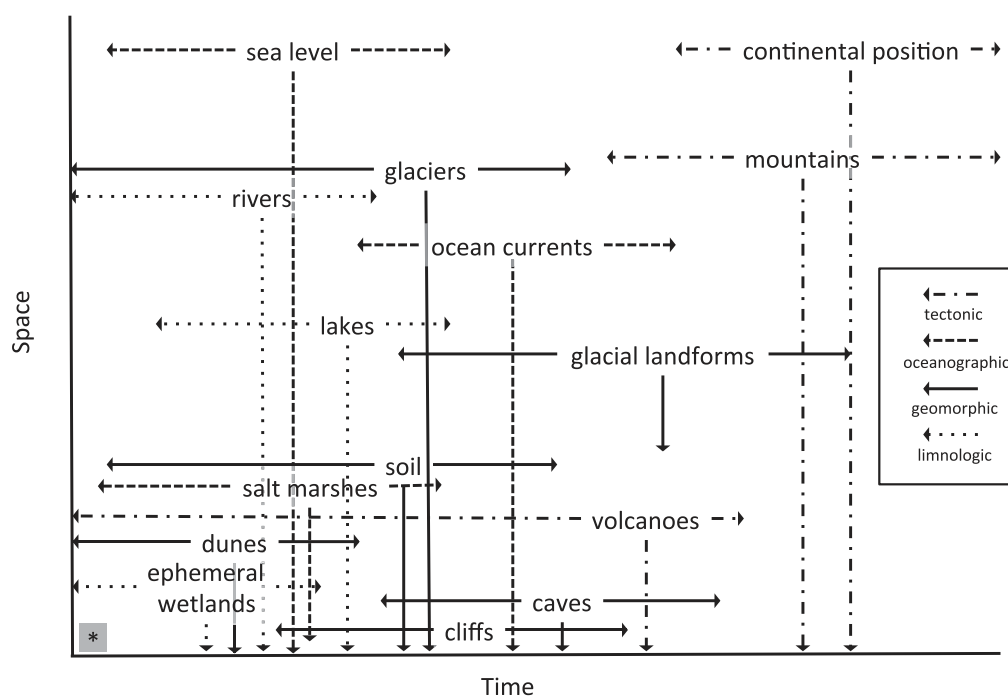


Figure 1. Durability of select landforms (dashed arrows, range of spatiotemporal durability of land facets; box with an asterisk, spatiotemporal scale of typical ecology and conservation research).

scales, and have been well connected with ecological diversity in both the past and present (Williams & Jackson 2007; Loarie et al. 2009; Sandel et al. 2011; Ohlemüller et al. 2012; Ordonez & Williams 2013). Climate velocity is related to topography (Loarie et al. 2009) and species endemism (Sandel et al. 2011) and provides the potential for understanding relationships between topography (a durable feature of the stage on shallow time scales) and biodiversity (which changes through time). A key avenue of future research is to establish links between present-day geophysical attributes, climate change, and biological processes (Ackerly et al. 2010).

The lesson of the paleorecord is one of both resilience and vulnerability and is characterized by equilibrium and disequilibrium responses. The Quaternary paleoecological record shows that communities are tenuous conservation units, assembling and disassembling through time as species respond individually to environmental change. A paleoecological perspective to conservation highlights two things. First, the dynamic nature of the past lends itself to a CNS approach by highlighting the fragility of species- and community-based conservation strategies. Second, because it considers matters over the long term, paleoecology provides a helpful perspective on the challenges and opportunities for conserving nature's stage in a dynamic landscape. Geodiversity-based conservation is a framework that explicitly acknowledges dynamic processes, including extinction, evolution, community turnover, and novelty. That is, it acknowledges change—not necessarily as a hindrance to conservation,

but as intrinsic properties of the very nature we aim to conserve.

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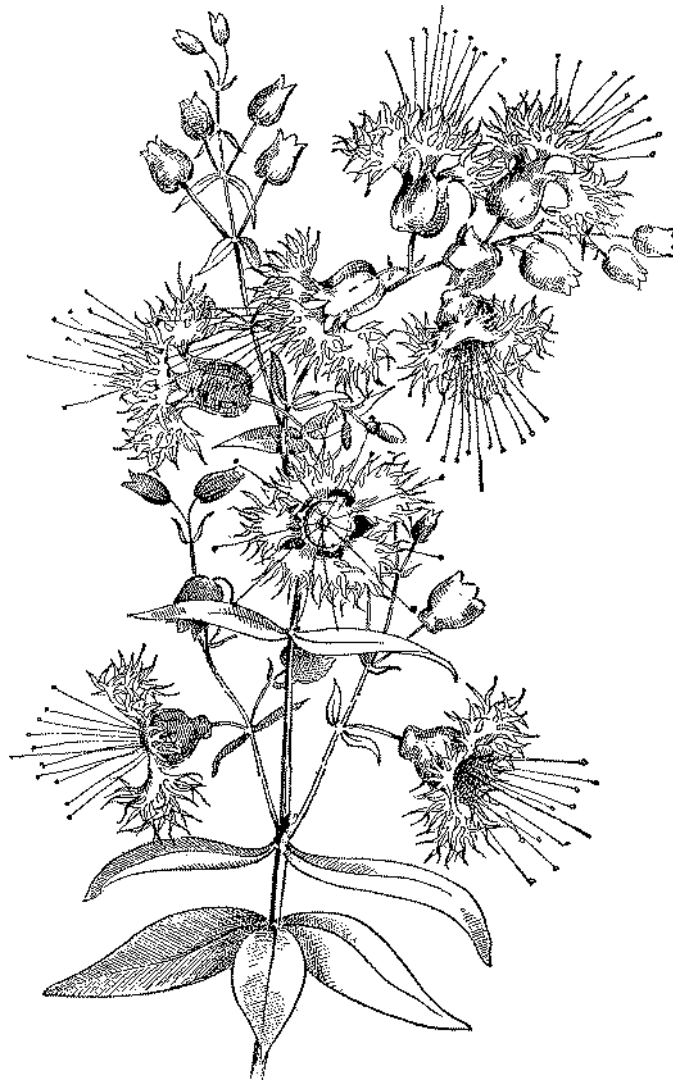
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Global status of and prospects for protection of terrestrial geophysical diversity

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Abstract: *Conservation of representative facets of geophysical diversity may help conserve biological diversity as the climate changes. We conducted a global classification of terrestrial geophysical diversity and analyzed how land protection varies across geophysical diversity types. Geophysical diversity was classified in terms of soil type, elevation, and biogeographic realm and then compared to the global distribution of protected areas in 2012. We found that 300 (45%) of 672 broad geophysical diversity types currently meet the Convention on Biological Diversity's Aichi Target 11 of 17% terrestrial areal protection, which suggested that efforts to implement geophysical diversity conservation have a substantive basis on which to build. However, current protected areas were heavily biased toward high elevation and low fertility soils. We assessed 3 scenarios of protected area expansion and found that protection focused on threatened species, if fully implemented, would also protect an additional 29% of geophysical diversity types, ecoregional-focused protection would protect an additional 24%, and a combined scenario would protect an additional 42%. Future efforts need to specifically target low-elevation sites with productive soils for protection and manage for connectivity among geophysical diversity types. These efforts may be hampered by the sheer number of geophysical diversity facets that the world contains, which makes clear target setting and prioritization an important next step.*

Keywords: climate adaptation, conservation planning, geodiversity, soil type, spatial assessment, topography

Condición Mundial y Perspectivas para la Protección de la Diversidad Geofísica Terrestre

Resumen: *La conservación de las facetas representativas de la diversidad geofísica puede ayudar a conservar la diversidad biológica conforme cambia el clima. Llevamos a cabo una clasificación mundial de la diversidad geofísica terrestre y analizamos la variación de la protección del suelo a lo largo de los tipos de diversidad geofísica. La diversidad geofísica se clasificó en términos de tipo de suelo, elevación y reino biogeográfico y después se comparó con la distribución global de las áreas protegidas en 2012. Encontramos que 300 (45%) de los 627 tipos generales de diversidad geofísica actualmente cumplen con el Objetivo Aichi 11 de la Convención sobre la Diversidad Biológica de 17% de protección de área terrestre, lo que sugiere que los esfuerzos por implementar la conservación de la diversidad geofísica tienen una base sustancial sobre la cual fundamentarse. Sin embargo, las áreas protegidas actuales fueron fuertemente parciales hacia los suelos de alta elevación y baja fertilidad. Evaluamos tres escenarios de la expansión de áreas protegidas y encontramos que la protección enfocada en especies amenazadas, si se implementa de lleno, también protegería a un 29% adicional de tipos de diversidad geofísica; la protección enfocada en eco-regiones protegería a un 24% adicional, y un escenario combinado protegería a un 42% adicional. Los esfuerzos futuros necesitan enfocarse específicamente en sitios de poca elevación con suelos productivos para la protección y manejarse para la conectividad entre los tipos de diversidad geofísica. Estos esfuerzos pueden dificultarse simplemente por el número de facetas de diversidad geofísica que existen en el mundo, lo cual hace que el establecimiento claro de objetivos y la priorización sean un siguiente paso importante.*

Palabras Clave: adaptación al cambio climático, evaluación espacial, geodiversidad, planeación de la conservación, tipo de suelo, topografía

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Introduction

The global protected area (PA) network is doing poorly at conserving most elements of biodiversity (Venter et al. 2014), and rapid human-forced climate change will likely exacerbate this problem (Johnston et al. 2013). In 2010, 193 nations responded to drastic shortfalls in PA coverage by setting an ambitious global target of protecting at least 17% of terrestrial areas and inland waters by 2020 (Aichi Target 11, CBD 2011), which could lead to the greatest and potentially the last substantial expansion of the PA estate (Watson et al. 2014). It is clearly vital that this expansion include placing new PAs or enlarging existing ones to increase biodiversity's resilience to current and future climate change (Hannah et al. 2007; Watson et al. 2013).

One promising approach lies in protecting representative facets of geophysical diversity itself, the stage on which biodiversity plays (Hunter et al. 1988; Anderson & Ferree 2010). The hypothesis is that even as the climate changes, geophysical diversity will continue to be important to species and ecosystem processes in the future, even if the species and processes are different than today (Cowling et al. 2003; Beier & Brost 2010).

Planning where to protect different types of geophysical diversity requires mapping them. Geophysical diversity has been mapped at regional scales by characterizing the abiotic condition (e.g., geological substrate, soil type, and topography) through the use of overlay methods (e.g., Pressey et al. 2000) or clustering algorithms (e.g., Brost & Beier 2012). Here we present the first (to our knowledge) framework for defining terrestrial geophysical diversity at the global scale. Although regional studies have been able to use higher resolution descriptions of abiotic condition (e.g., slope, aspect, and ruggedness, Anderson et al. 2015 [this issue]), these variables cannot be meaningfully resolved using global data sets with cell resolutions measured in minutes of latitude and longitude. Similarly, global maps of geomorphological features like drumlins, deltaic fans, and moraines do not exist. Our map is based solely on geodiversity elements like landform and lithology and thus differs from ecological land unit maps (e.g., Sayre et al. 2014) that additionally reflect climate and land cover.

We defined and mapped global terrestrial geodiversity at approximately 3.4 km resolution using 3 well-mapped variables: soil type, elevation, and biogeographic realm. Soils reflect the surface aspect of geophysical diversity that species directly experience and are developed through long-term interactions between topography, vegetation, lithology, and historical climatic regimes (Jenny 1941; Singer & Munns 2005). Land surface elevation affects the amount of incident solar radiation and drives temperature gradients through adiabatic cooling. Biogeographic realm is a surrogate for latitude

and the distribution of continental landmasses as reflected by important biogeographic boundaries like Wallace's Line and the Central American isthmus. These 3 factors generate a set of relatively uniform geophysical diversity types (GDTs), which are further composed of separate geophysical diversity facets (GDFs). We analyzed the extent to which these GDTs and GDFs are currently protected. We also assessed how well recent species-based and ecoregion-based global prioritizations capture GDTs to inform development of a global, climate-adapted, geophysical diversity-based conservation strategy in light of the CBD Aichi Target 11.

Methods

Mapping Global Geophysical Diversity

We overlaid data in a geographic information system (GIS) on the distribution of 7 biogeographic realms (Olson et al. 2001) elevation, and soil types to generate GDTs. Elevation data were obtained from the Shuttle Radar Topography Mission (NGIA & NASA 2009), which provides height above the mean sea level at 0.0083 degree resolution on a geographic coordinate system. We reclassified elevations into 11 elevation zones at 500 m increments (e.g., 0–499 m) up to 4999 m, lumping elevations 5000–8204 m into a 12th zone. Although some regional maps set elevation bands to match patterns of vegetation (Anderson et al. 2015), no single set of elevation bands is appropriate for the entire globe.

Soil typology was based on the taxonomy developed by the U.S. Department of Agriculture (Soil Survey Staff 1999). We used soil orders (mollisols, alfisols, histosols, etc.) that represent variation in long-term patterns of weathering, parent material, dominant vegetation, accumulated organic material, and climatic condition. These are analogous to classes in animal taxonomy (e.g., birds and mammals) and represent distinctive and significant variation in soil types (Singer & Munns 2005). The U.S. Natural Resource Conservation Service (2005) describes the spatial location and extent of 12 soil orders and 4 types of other substrates (Table 1 & Supporting Information) on grid cells of 2-min resolution. We did not explicitly include a lithology map because parent material (i.e., geological substrate) is an input to the soil classification.

All the data were re-projected to the planar Goode homolosine map projection (GHSP) on the WGS84 datum with land-oriented interruptions as defined by ESRI (2008) and resampled with the nearest neighbor method, appropriate for categorical data, to a grid cell size of 3454 m (the average global resolution of the soil data). We included only terrestrial cells that had values from all 3 data sets.

Table 1. Descriptions of 4 substrate types and 12 soil of the world (Soil Survey Staff 1999; U.S. Natural Resources Conservation Service 2005) and representative examples of protected areas that cover them in part.

<i>Substrate or soil order</i>	<i>Description</i>	<i>Representative protected area</i>
Shifting sand	moving sands with little or no soil development	Central Kalahari Game Reserve, Botswana; Munga-Thirri National Park, Australia
Rock	undecomposed surface rocks with little or no soil development	Aconcagua Provincial Park, Argentina; Badakhshan National Park, Tajikistan; Yosemite National Park, U.S.A.
Ice	surface ice fields with little or no soil development	Northeast Greenland National Park, Denmark; Russian Arctic National Park, Russia; Sagarmatha National Park, Nepal
Undefined	unknown	Bakhtegan National Park, Iran; Pampa del Tamarugal National Reserve, Chile
Gelisols	form in very cold climates with permafrost within 2 m of the soil surface; typically support tundra type vegetation	Jungfrau-Aletsch-Bietschhorn UNESCO World Heritage Site, Switzerland; Northeast Greenland National Park, Denmark; Wapusk National Park, Canada
Histosols	organic soils formed either in cool climates or very wet areas or a combination of both; often associated with bogs or swamps even after the land has been drained	Ben Nevis and Glen Coe National Scenic Area, UK; Berbak National Park, Indonesia; Everglades National Park, U.S.A.
Spodosols	typical of both coniferous and deciduous forests in cooler climates and some heathlands; typically have a rich organic layer over a highly leached sand or mineral layers	Algonquin Provincial Park, Canada; Parc Naturel Régional des Landes de Gascogne, France; Putoransky State Nature Reserve, Russia
Andisols	dominated by minerals derived from volcanic ash; typically weakly weathered with a high content of volcanic glass	Nahuel Huapi National Park, Argentina; Volcans National Park, Rwanda
Oxisols	highly weathered soils of the tropics; similar to ultisols but more weathered such that nutrient content and carbon content is low; some oxisols have been previously classified as laterite soils	Parc National de la Salonga, Democratic Republic of Congo; Vale do Javari Indigenous Area, Brazil
Vertisols	contain a high proportion of expanding lattice clays so tend to swell when wet and shrink up drying	Attwater Prairie Chicken National Wildlife Refuge, U.S.A.; Oberpfälzer Wald Naturpark, Germany
Aridosols	develop in very dry conditions; surface patterns may show the effects of extreme wetting and drying events but with little evidence of moisture penetration to the subsoil	Death Valley National Park, U.S.A.; Dundas Nature Reserve, Australia; Parque Nacional Natural Macuira, Colombia
Ultisols	most weathered of the temperate zone soils; characterized by a thin or absent surface horizon with a thick, strongly expressed B horizon; deep and can be productive if well-managed; often red or orange in color	Capitol Reef National Park, U.S.A.; Ruaha National Park, Tanzania; Zona de Amortiguamiento (Bosawas) Biosphere Reserve, Nicaragua
Mollisols	deep, dark, nutrient rich layer at the surface; typically form under temperate grassland vegetation as the result of the long-term addition of organic materials derived from plant roots; make productive cropland	Dongying-Huang He Sanjiaozhou Nature Reserve, China; Hawkeye State Wildlife Management Area, U.S.A.; Sjeverni Velebit National Park, Croatia
Alfisols	intermediate in maturity between mollisols or spodosols and ultisols; often found in co-occurrence with mollisols; more weathered than mollisols and generally have less weatherable material remaining	Kaimur Wildlife Sanctuary, India; Parc Naturel Régional Périgord Limousin, France; Waterloo State Recreation Area, Michigan, U.S.A.
Inceptisols	earliest indications of horizon development; small amounts of organic matter darken the topmost horizon; weathering minimal; high amounts of weatherable minerals remain in profile	Dasos Pafou Special Protection Area, Cyprus; Luengué Hunting Reserve, Angola; Serengeti National Park, Tanzania
Entisols	very young soils formed from freshly deposited or heavily reworked material like flood deposits or sand dunes	Naybandan Wildlife Refuge, Iran; Sian Ka'an UNESCO-MAB Biosphere Reserve, Mexico; Yellowstone National Park, U.S.A.

We combined the 3 raster data sets by assigning numeric codes to each realm, elevation zone, and soil order type. We used magnitude to differentiate the input data (i.e., soil codes were multiplied by 10,000, elevation codes by 100, and realm by 1) and added the codes to create a unique code for

each GDT (e.g., code 10201 represents 0–499 m, Australasian shifting sands). To examine the size of individual facets, we converted rasters to polygons, creating regions of contiguous cells of the same GDT, which were labeled and analyzed as geophysical diversity facets (GDFs).

Characterization of Areal Protection for Geophysical Diversity

Terrestrial PA boundaries were obtained from the World Database on PAs (IUCN and UNEP 2012). Following Venter et al. (2014), we included only PAs with national designations. In the database, PAs are represented either as polygons or by point locations with an associated area. For PAs represented only by points, we created a circular buffer of the given area centered on the location. Buffered PA points and polygons were merged into a single layer to remove overlaps. After re-projecting to the GHSP, we tabulated areas of intersection with the GDTs. We conducted GIS work with ArcGIS 10.1 and plotted graphs in R (R Core Team 2014).

Assessment of Future Possible Protection Scenarios

Using the data available in Venter et al. (2014), we assessed how 3 future scenarios for expansion of PAs would increase the levels of coverage afforded to GDTs: adequate capture of all globally threatened bird and amphibian targets (hereafter species scenario); capture of 17% of all terrestrial ecoregions (hereafter ecoregion scenario); and a combined prioritization that achieved both species and ecoregion targets (hereafter combined scenario). New PAs identified in each of the 3 scenarios were re-projected to the GHSP and overlaid on the GDTs to assess additional coverage afforded by the PA expansion scenario.

Results

We mapped 672 global geophysical diversity types (GDTs) ranging in total area from 12 km² to 5.4 million km² (Supporting Information). Some combinations of soil order, elevation, and biogeographic realm produced a GDT with a non-zero area (Fig. 1). Of the biogeographic realms, the Palearctic had the most (138 GDTs), while Oceania had the least (29 GDTs). The GDTs generally declined in area as elevation increased, although not in all cases (e.g., particularly gelisols, rock, and ice types).

The single most extensive single GDT in the world was the low elevation (0–499 m) Palearctic Inceptisols, which covered approximately 4% of the land's surface (outside Antarctica) and was associated with the extensive boreal forest ecosystems of northern Eurasia. Most GDTs were much smaller in extent: 29% were <1000 km² in area, 50% were <10,000 km², 79% were <100,000 km², and 95% were <1 million km². The next 3 most extensive types were the 0–499 m Palearctic Entisols (4.9 million km²), distributed mainly in the Sahara Desert and the Rub' al Khali (Empty Quarter) of the Arabian Peninsula; the 0–499 m Neotropical Oxisols (4.7 million km²) of the Amazon Basin and other tropical forests of South America; and

the 0–499 m Palearctic Gelisols (3.6 million km²) of the northern Siberian plain.

We mapped 418,511 global geophysical diversity facets (GDFs), which are areas of contiguous cells that are homogenous with respect to biogeographic realm, elevation zone, and soil type. The GDTs varied in the number of GDFs they contained. Each of 39 types had only 1 facet globally, while conversely the 500–999 m Palearctic Inceptisol GDT had 13,862 facets (Supporting Information). Within GDTs, the average size of facets varied from 12 km² for 50 of the types to 30,665 km² for the 0–499 m Indo-Malay shifting sands, which had only 1 very large tract: the Thar Desert of India and Pakistan. About 66% of GDTs had average facet sizes of <100 km²; 93% had average facet sizes of <1000 km²; and all but 1 had average facet sizes of <10,000 km².

Only 68 (10.1%) of 672 GDTs have no PA coverage, and 300 (44.6%) of GDTs met the 17% CBD Aichi Target 11 (Table 2). Forty-five types were >90% protected, each of which had small extent (average of 285 km²). Protection was skewed toward higher elevations and less productive soil types (particularly ice and gelisols). Topographically rugged areas, which are often well protected, were also richer in GDTs of smaller extents, which may help explain why so many of montane types already met the 17% goal. The least protected soil types globally were mollisols (3.4%), undefined soil types (5.4%; mainly in south-central Asia and South America), and vertisols (6.5%). Mollisols, in particular, are noted for their agricultural productivity (Singer & Munns 2005); they were currently best protected in Australasia (12.3%) and least protected in Oceania (1.3%). Interestingly, all GDTs below 3000 m had yet to meet Aichi Target 11; all above already surpassed it (Table 2).

When future PA expansion scenarios based on either species-based targets, ecoregion-based targets, or a combination of both were considered, the number of GDTs meeting 17% coverage targets increased (Table 3). The species-based prioritization would protect another 197 GDTs at the 17% level, whereas the ecoregional scenario would add 158 GDTs. The combined scenario would add 279 GDTs at the 17% level, leaving only 18 GDTs insufficiently protected, but this scenario almost doubled the global PA estate (Table 3). The species-focused prioritization appeared to perform better than the ecoregional one because of the interaction of cost (based on the value of agricultural land) and how area goals were set (see Venter et al. 2014). Species prioritization favored selection of places where range-limited species predominated (e.g., on islands), whereas large ecoregions provided more flexibility to lower costs by avoiding productive and therefore, expensive, soil types, allowing fewer GDTs to be covered. This result is important because many nations are currently using ecoregional coverage targets as a way to plan future expansion of their PA estate (Watson et al. 2014).

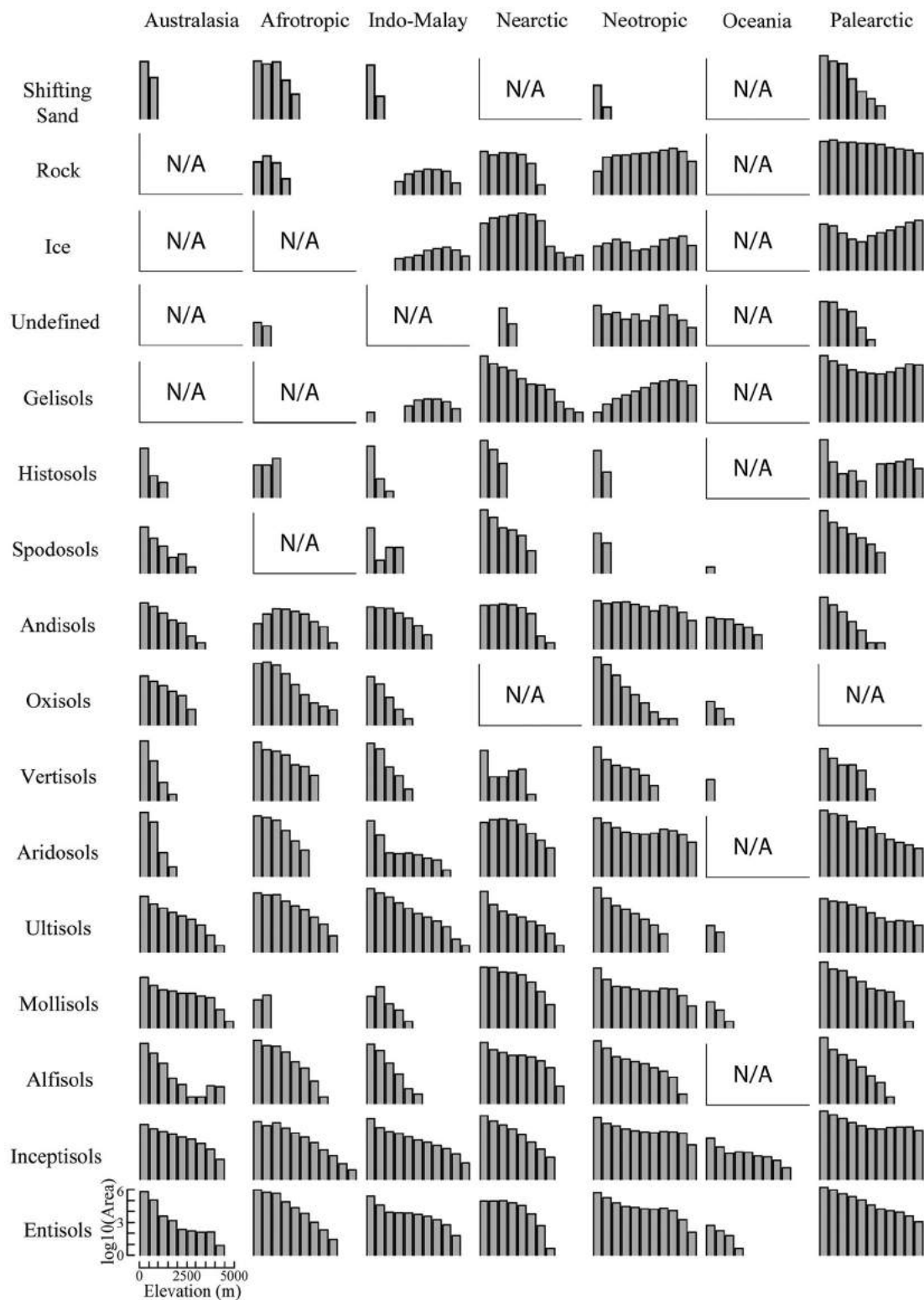


Figure 1. Differences in area (square kilometers on a log10 scale) of geophysical diversity types for combinations of soil type, biogeographic realm, and elevation. Each panel represents a combination of soil type (y-axis) and biogeographic realm (x-axis); units of measure are shown on the lowest left panel. Panels with N/A indicate combinations of soil type and biogeogeographic realm that do not exist; lack of elevation bars indicates combinations of soil type, biogeographic realm, and elevation that do not exist.

Table 2. Percentage of the area of each geophysical diversity type protected in 2012 (IUCN & UNEP 2012).^a

Aspect of geophysical diversity	Soil order or substrate type																
	Shifting sands	Rock	Ice	Undefined	Gelisols	bistosols	spodosols	andisols	oxisols	vertisols	aridosols	ultisols	mollisols	alfisols	inceptisols	entisols	Totals
Elevation bands (m)																	
0 – 499	11.0	3.5	40.6 ^b	5.7	15.3	8.1	7.1	10.2	30.9 ^b	5.7	7.1	14.9	2.5	7.4	11.8	9.6	11.3
500 – 999	15.7	8.9	40.7 ^b	5.7	15.7	3.2	11.7	17.3 ^b	13.6	9.2	9.6	15.6	3.8	10.5	11.4	11.6	11.8
1000–1499	13.5	12.6	35.4 ^b	3.1	19.1 ^b	14.9	26.5 ^b	21.2 ^b	15.9	15.9	10.5	21.5 ^b	4.6	10.6	16.4	13.7	14.5
1500–1999	9.9	11.4	42.1 ^b	23.5 ^b	20.6 ^b	<0.1	21.1 ^b	21.3 ^b	10.1	8.6	7.0	11.5	5.2	9.9	15.7	9.0	13.0
2000–2499	<0.1	12.1	39.4 ^b	8.3	19.3 ^b	<0.1	24.7 ^b	21.8 ^b	34.3 ^b	7.4	6.5	16.1	7.3	11.2	16.3	7.2	16.5
2500–2999	<0.1	6.6	44.0 ^b	1.7	21.5 ^b	NA	32.4 ^b	25.4 ^b	65.0 ^b	2.0	5.8	28.7 ^b	11.5	16.1	16.8	8.3	21.0 ^b
3000–3499	<0.1	6.4	53.8 ^b	<0.1	22.7 ^b	54.0 ^b	85.0 ^b	36.5 ^b	76.7 ^b	6.6	15.4	37.0 ^b	21.3 ^b	30.1 ^b	20.3 ^b	9.9	22.0 ^b
3500–3999	NA	7.2	17.3 ^b	0.7	22.4 ^b	46.8 ^b	NA	8.1	92.9 ^b	NA	19.2 ^b	42.1 ^b	11.8	39.6 ^b	23.3 ^b	10.6	17.9 ^b
4000–4499	NA	11.9	26.2 ^b	8.1	42.6 ^b	83.2 ^b	NA	12.6	100.0 ^b	NA	23.0 ^b	29.4 ^b	5.4	25.6 ^b	21.8 ^b	10.7	26.9 ^b
4500–4999	NA	14.9	42.1 ^b	3.3	58.5 ^b	23.5 ^b	NA	24.5 ^b	NA	NA	19.4 ^b	14.7	11.1	100.0 ^b	19.1 ^b	14.5	43.0 ^b
> 5000	NA	21.1 ^b	44.4 ^b	8.3	51.9 ^b	11.9	NA	50.9 ^b	NA	NA	17.9 ^b	9.0	40.0 ^b	NA	16.4	30.9 ^b	44.6 ^b
Realm																	
Afrotropic	15.4	<0.1	NA	<0.1	NA	14.0	NA	20.0 ^b	11.6	11.9	12.6	18.6 ^b	4.8	14.2	18.4 ^b	12.9	13.9
Australasia	25.8 ^b	NA	NA	NA	NA	23.2 ^b	39.0 ^b	16.1	16.5	3.6	7.7	16.0	12.5	7.2	16.6	12.7	11.4
Indo-Malay	21.1 ^b	8.1	46.6 ^b	NA	50.0 ^b	9.9	16.6	23.9 ^b	10.0	3.2	8.1	12.2	4.5	5.4	5.4	8.2	9.1
Nearctic	NA	26.7 ^b	41.4 ^b	0.5	19.2 ^b	6.7	7.9	26.4 ^b	NA	1.1	8.8	3.8	3.3	5.1	17.7 ^b	11.5	13.8
Neotropic	69.3 ^b	9.8	35.2 ^b	3.5	17.5 ^b	23.1 ^b	0.2	15.5	33.7 ^b	8.6	8.0	24.2 ^b	5.0	9.5	23.7 ^b	11.5	20.9 ^b
Oceania	NA	NA	NA	NA	NA	NA	<0.1	12.7	<0.1	<0.1	NA	<0.1	1.3	NA	7.2	4.1	7.5
Palaearctic	7.1	8.1	39.6 ^b	7.2	21.2 ^b	5.7	7.6	6.6	NA	5.4	7.1	7.9	2.8	5.2	9.3	8.6	9.5
Totals	12.3	9.3	41.0 ^b	5.4	20.4 ^b	8.5	8.2	16.3	24.5 ^b	6.5	8.3	15.7	3.4	8.3	13.1	10.6	12.9

^aAn NA indicates the combination of soil type and elevation or soil type and biogeographic realm does not exist.^bExceeds Aichi target of 17%.

Table 3. Benefits of 3 future protection scenarios (based on Venter et al. [2014]) for terrestrial geophysical diversity type (GDT) coverage.

Protection scenario	Size of protected area (PA) estate as a percentage of global terrestrial area	Number of GDTs meeting or exceeding 17% target (%)	Number of GDTs not meeting 17% target (%)	Number of GDTs with no representation in global PA estate (%)
Current (circa 2012)	12.9	300 (44.6)	372 (55.4)	68 (10.1)
Species ^a	18.1	497 (74.0)	175 (26.0)	23 (3.4)
Ecoregion ^b	21.1	458 (68.2)	214 (31.8)	44 (6.5)
Combined ^c	23.1	579 (86.2)	93 (13.8)	18 (2.7)

^aExpansion of protected areas (PAs) that meets representation targets for threatened terrestrial birds, mammals, and amphibians.

^bExpansion of PAs meets or exceeds 17% of all terrestrial ecosystems.

^cExpansion of PAs meets both species and ecoregion targets.

Discussion

Advancing a geophysical diversity conservation strategy requires an operational definition of geophysical diversity on the global scale and the assessment of current conservation efforts for areas of different geophysical diversity types. We highlighted some practical problems that future geophysical diversity conservation planners should consider. One problem was the sheer number of GDTs (672) at the global scale. Although increasing the number of variables and the number of classes per variable would better describe global geophysical diversity, this would lead to thousands of GDTs. A large number of types can be difficult to interpret or explain to stakeholders and implementers (Beier & Brost 2010). Planning for conservation of geophysical diversity at regional extents (as is typically the case [Anderson et al. 2015]) naturally focuses on locally relevant geophysical characteristics and a manageable number of types. Limiting the extent, however, creates potential boundary issues and does not address the fact that climate change is a global, not a regional, conservation problem.

The current geography of protection presented here provides a useful starting point for conservation of terrestrial geophysical diversity. Relatively few (~ 10%) geophysical diversity types existed without at least some modicum of protection, and 300 types (44%) were already protected at the Aichi Target 11 level of 17%. Like other studies (e.g., Joppa & Pfaff 2009), we found a bias toward protecting soil types and elevation zones that were less productive or less suitable for human habitation. It seems unlikely that these general findings would be affected by a different choice of soil classification or a different set of intervals dividing elevation.

We also showed that if global PA prioritizations based on meeting species and ecoregion targets were enacted, geophysical diversity would be more protected, but not entirely protected (Table 3). These results will have ramifications for how nations address CBD Aichi Target 11 in the future because species and ecoregional coverage targets could be met without conserving all of geophysical diversity. Our results indicate that conservation planners should look for opportunities to prioritize low elevation

areas and productive soil types like mollisols, vertisols, and alfisols, which may mean turning more attention to cities, suburbs, and agricultural areas, where most of these soil types are found. As competition for this type of land is often fierce, systematic planning approaches that address opportunity, efficiency, and complementarity will be necessary to ensure conservation gains can be achieved (Carwardine et al. 2008).

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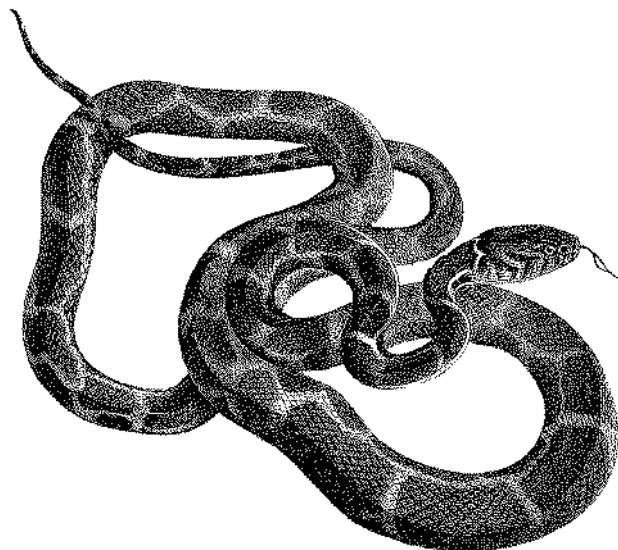
Supporting Information

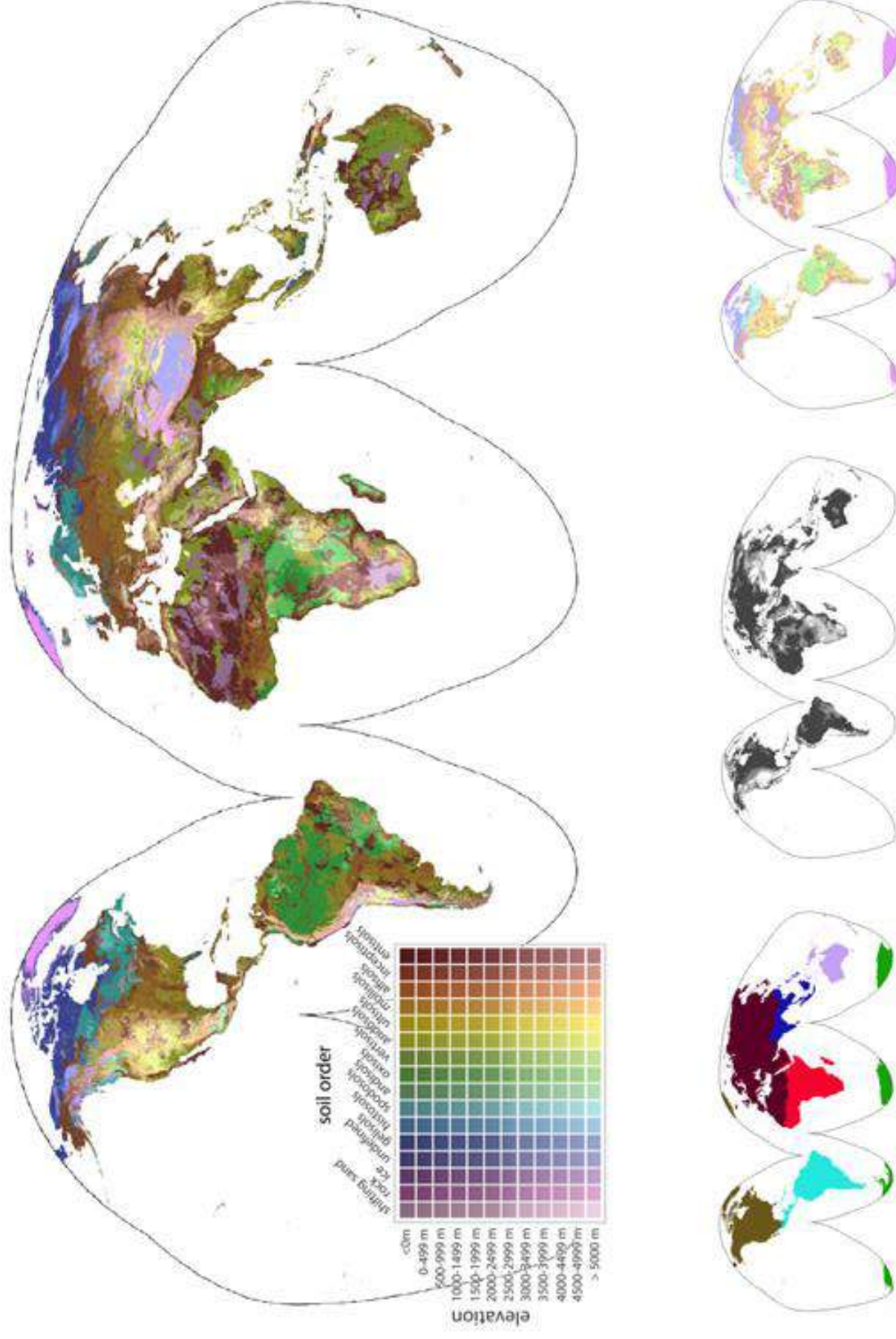
A color figure showing the global distribution of terrestrial GDTs and their constituent elements (e.g., soil orders, elevation zones, and biogeographic regions) (Appendix S1) and a complete list of GDTs with summary statistics on area and number and area of facets (Appendix S2) are available online. 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.

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The effectiveness of marine reserve systems constructed using different surrogates of biodiversity

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Abstract: *Biological sampling in marine systems is often limited, and the cost of acquiring new data is high. We sought to assess whether systematic reserves designed using abiotic domains adequately conserve a comprehensive range of species in a tropical marine inter-reef system. We based our assessment on data from the Great Barrier Reef, Australia. We designed reserve systems aiming to conserve 30% of each species based on 4 abiotic surrogate types (abiotic domains; weighted abiotic domains; pre-defined bioregions; and random selection of areas). We evaluated each surrogate in scenarios with and without cost (cost to fishery) and clumping (size of conservation area) constraints. To measure the efficacy of each reserve system for conservation purposes, we evaluated how well 842 species collected at 1155 sites across the Great Barrier Reef seabed were represented in each reserve system. When reserve design included both cost and clumping constraints, the mean proportion of species reaching the conservation target was 20–27% higher for reserve systems that were biologically informed than reserves designed using unweighted environmental data. All domains performed substantially better than random, except when there were no spatial or economic constraints placed on the system design. Under the scenario with no constraints, the mean proportion of species reaching the conservation target ranged from 98.5% to 99.99% across all surrogate domains, whereas the range was 90–96% across all domains when both cost and clumping were considered. This proportion did not change considerably between scenarios where one constraint was imposed and scenarios where both cost and clumping constraints were considered. We conclude that representative reserve systems can be designed using abiotic domains; however, there are substantial benefits if some biological information is incorporated.*

Keywords: abiotic domain, conservation planning, conserving nature's stage, inter-reef seabed, reserve design

La Efectividad de los Sistemas de Reservas Marinas que Utilizan Sustitutos de la Biodiversidad Diferentes

Resumen: *El muestreo biológico en los sistemas marinos generalmente es limitado, y el costo de adquirir nuevos datos es alto. Buscamos evaluar si las reservas sistemáticas diseñadas usando dominios abióticos conservan adecuadamente una gama completa de especies en un sistema marino tropical inter-arrecifal. Basamos nuestra evaluación en datos de la Gran Barrera de Coral, Australia. Diseñamos sistemas de reservas con miras a conservar el 30% de cada especie, con base en cuatro tipos de sustitutos abióticos (dominios abióticos; dominios abióticos sopesados; bioregiones pre-definidas; y selección azarosa de áreas). Evaluamos a cada sustituto en escenarios con y sin costos (costo para la industria pesquera) y restricciones de amontonamiento (tamaño del área de conservación). Para medir la eficiencia de cada sistema de reservas para propósitos de la conservación, evaluamos cuán bien representadas fueron 842 especies colectadas en 1155 sitios en cada sistema de reservas a lo largo del lecho marino de la Gran Barrera de Coral. Cuando el diseño de la reserva incluyó tanto al costo como a las restricciones de amontonamiento, la proporción media de especies que alcanzó el objetivo de conservación fue 20–27% más alta para los sistemas de reservas que fueron informados biológicamente que para las reservas diseñadas usando datos ambientales sin peso.*

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Todos los dominios se desempeñaron sustancialmente mejor que el azar, excepto cuando no hubo restricciones espaciales o económicas puestas sobre el diseño del sistema. Bajo este escenario sin restricciones, la proporción media de las especies que alcanzó el objetivo de conservación se ubicó en un rango de 98.5% y 99.99% a lo largo de todos los dominios sustitutos, mientras que el rango fue de 90–96% a lo largo de todos los dominios cuando se consideraron el costo y el amontonamiento. Esta proporción no cambió considerablemente entre los escenarios en los que se impuso una restricción ni en los escenarios en los que tanto el costo como las restricciones de amontonamiento fueron considerados. Concluimos que los sistemas representativos de reservas pueden diseñarse usando dominios abióticos; sin embargo, hay beneficios sustanciales si se incorpora alguna información biológica.

Palabras Clave: conservar el estado de la naturaleza, diseño de reservas, dominio abiótico, lecho marino interarrecifal, planeación de la conservación

Introduction

Reserves are implemented to protect and ensure the persistence of community structure, genetic diversity, and species diversity. To achieve this goal, a portion of all species, communities, or features of interest within a reserve system should be represented at sufficient levels to conserve those features into the future. Conservation reserves have not always been designed with species representation as a priority and have traditionally been placed primarily in areas with little economic value (Pressey et al. 1993). The notion of complementarity—selecting sites for reservation that complement the sites that have already been selected—provides a general process for building representative reserve systems efficiently (Margules & Pressey 2000). The complementarity approach selects areas with the most different faunal and floral compositions from sites that are already conserved in order to maximize biodiversity conservation. This contrasts with the idea of choosing areas with high local species biodiversity. Areas with high local diversity may have similar species composition, whereas areas with unique species composition but low overall species diversity may be overlooked if complementarity is not considered. This would result in lower overall representation of biodiversity and thus lessen the ability of the reserve system to maximize biodiversity protection (Moilanen et al. 2009).

To build a representative reserve system, we would ideally like to know the distribution of all species of interest. The trade-off between prolonging the design process in order to collect biological data and implementing reserves rapidly to protect diversity is the subject of considerable debate (e.g., Grantham et al. 2009; Weeks et al. 2010; Runting et al. 2013). The cost of collecting extensive biological data can be prohibitive in many countries, either in terms of time or money. Where there are biological data available for designing marine reserves, sampling is often not comprehensive across taxonomic groups (Pinto & Bini 2008). Ultimately, reserve systems are designed using incomplete information and typically involve the use of alternative surrogates for biodiversity (Caro & O'Doherty 1999).

Surrogates can be classified into three broad classes—biological surrogates, habitat surrogates, and abiotic surrogates. Biological surrogates range from a single indicator species to a species group that is assumed to represent all other species groups for which there are little to no data (De Cáceres & Legendre 2009; Mokany et al. 2011). These have been used in conservation with mixed success (e.g., Beger et al. 2007; Larsen et al. 2009; Grantham et al. 2010).

Habitat surrogates can also be used to design reserve systems (Klein et al. 2008; Dalleau et al. 2010; Grantham et al. 2011, but see Stevens & Connolly 2004); a portion of each habitat class is included within a reserve system. The assumption is that different habitats represent different species composition and that the inclusion of a range of habitats will produce a representative reserve system (e.g. Ferrier et al. 2002). This has not yet been verified or tested for a comprehensive range of taxa and requires a substantial amount of data to determine habitat classes. Alternatively, mapped abiotic variables have been used to divide a region into a range of abiotic domains (Belbin 1993; Leathwick et al. 2003; Thieme et al. 2007). Domains defined by abiotic variables are relatively inexpensive and thus are attractive surrogates in reserve design (Beier & Brost 2010). This approach which can be referred to as ‘conserving nature’s stage’ has rarely been tested in marine systems and has never been tested using data comprehensively spanning the diversity of marine phyla. Abiotic domains are one way to differentiate areas within a region from others based on differences in abiotic variables (Coops et al. 2009; Terauds et al. 2012). Abiotic variables are often selected subjectively, and it is often assumed that the variables chosen have a large effect on biological responses across a range of taxonomic groups. Alternatively, all available variables can be used. Each variable may be weighted equally, to contribute equally toward the definition of the domain. However, abiotic variables rarely have equal influence on biological responses. Therefore, weighting the variables based on prior knowledge of biological influence may improve the effectiveness of surrogates, but it requires biological data for at least part of the area of interest, where abiotic data are also available (see Leathwick et al. 2011).

The fundamental assumption behind this approach is that biodiversity responds to abiotic gradients in such a way that biological composition is more similar within a domain than between domains and that the reserves that have been designed based on these domains would represent biodiversity. Where this has been previously tested, the biological data used to evaluate the reserves designed based on abiotic domains represented few taxonomic groups (Lombard et al. 2003; Ban 2009) or incorporated very few species within each taxonomic group (e.g. Januchowski-Hartley et al. 2011). These few studies suggest that abiotic surrogates should be used with extreme caution. There is therefore a need for a thorough investigation of the use of abiotic surrogates in conservation planning.

An opportunity to test the biological representativeness of reserves designed using abiotic domains is provided by a spatially and taxonomically comprehensive data set from the inter-reef seabed of the Great Barrier Reef, Australia (Pitcher et al. 2007). We used abiotic domains delineated through 3 different methods to design a reserve system for the Great Barrier Reef. We subsequently tested how well the domains represented 842 species from 11 phyla relative to randomly selected reserve systems using both observed and predicted species distributions. First, we constructed domains using equally weighted, readily accessible abiotic variables. Second, we constructed domains that included a wider range of abiotic variables weighted according to biological importance (Pitcher et al. 2012). Third, we used the bioregions currently defined by the Great Barrier Reef Marine Park Authority (GBRMPA) to evaluate the efficacy of reserve design using this method. We also tested the effect of incorporating 2 types of realistic constraints, namely, minimizing opportunity cost to commercial fisheries and clumping cells to produce a compact and more manageable reserve.

Methods

Biological Data

The Great Barrier Reef is a World Heritage Area that spans 348,000 km² and is composed of reefs, islands, inter-reef seabed, continental slope, and deep oceanic waters. The inter-reef seabed constitutes more than 60% of the total area (Great Barrier Reef Marine Park Authority 2009) and was sampled extensively by the Seabed Biodiversity Project (Pitcher et al. 2007) between 2003 and 2006. More than 70,000 site-by-species records of 4,723 species in 15 phyla were collected from 1189 sites with an epibenthic sled. Depths sampled ranged from 7 m near the coast, to 12 m over shoals, and to 105 m at the deepest point. The epibenthic sled had a steel frame (1 m long, 1.5 m wide, and 0.5 m high) and was fitted with 20 mm steel mesh panels and a 25 mm stretched-

Table 1. Number of species within each phylum collected with an epibenthic sled at 1189 sites across the Great Barrier Reef (GBR) and the predicted number of species expected across the GBR study area based on data from collections made with epibenthic sleds and trawl apparatus.

<i>Phylum</i>	<i>Number of species collected by epibenthic sled</i>	<i>Predicted number of species</i>
Annelida (segmented worms)	0	3
Arthropoda (crustaceans)	169	147
Brachiopoda (lampshells)	0	1
Bryozoa (lace corals)	84	124
Chlorophyta (green algae)	58	32
Chordata (fishes)	84	175
Cnidaria (jellyfish and corals)	34	43
Cyanophyta (bacteria)	0	1
Echinodermata (sea stars, sea cucumbers, urchins and brittle stars)	102	84
Foraminifera (forams)	0	1
Magnoliophyta (plants)	7	5
Mollusca (molluscs)	146	117
Phaeophyta (brown algae)	14	11
Porifera (sponges)	99	68
Rhodophyta (red algae)	45	25
Unidentified	0	1
Total	842	838

mesh net. It was deployed for 200 m at each site at a speed of 2 knots.

Almost 40,000 site-by-species records of 3,510 species representing 12 phyla were collected from 457 sites with trawl apparatus. The trawl was a single high-flying Florida Flyer net with a rope length of 8 fathoms and stretched mesh size of 50 mm. The net was towed in a straight line for 1 km at each of the 457 sites at a speed of 2.7 knots. All trawling was done at night, from 1 h after sunset until dawn, to align with commercial trawling efforts. All samples were photographed, and large specimens were processed immediately. The remainder of each sample was then subsampled, unless the catch was very small and the entire sample could be retained.

All specimens retained were identified, weighed, and counted. For this study, sites sampled by the trawl apparatus were too sparse to be used to quantify the effectiveness of reserves. Therefore, sled data were used for the observed species evaluation. Sites were chosen to ensure that the average distance between sites did not exceed 12 kms for spatial autocorrelation optimization (Pitcher et al. 2007). Species that occurred at <1% of sites were excluded from the analysis. This was done because these sites would have affected the site selection algorithm substantially and hence the results. However, they did not contribute substantially to the formation of domains in a conservation planning context. From a total of 1189 sites, we excluded 34 sites composed entirely of species that occurred at < 1% of sites. The biomass of

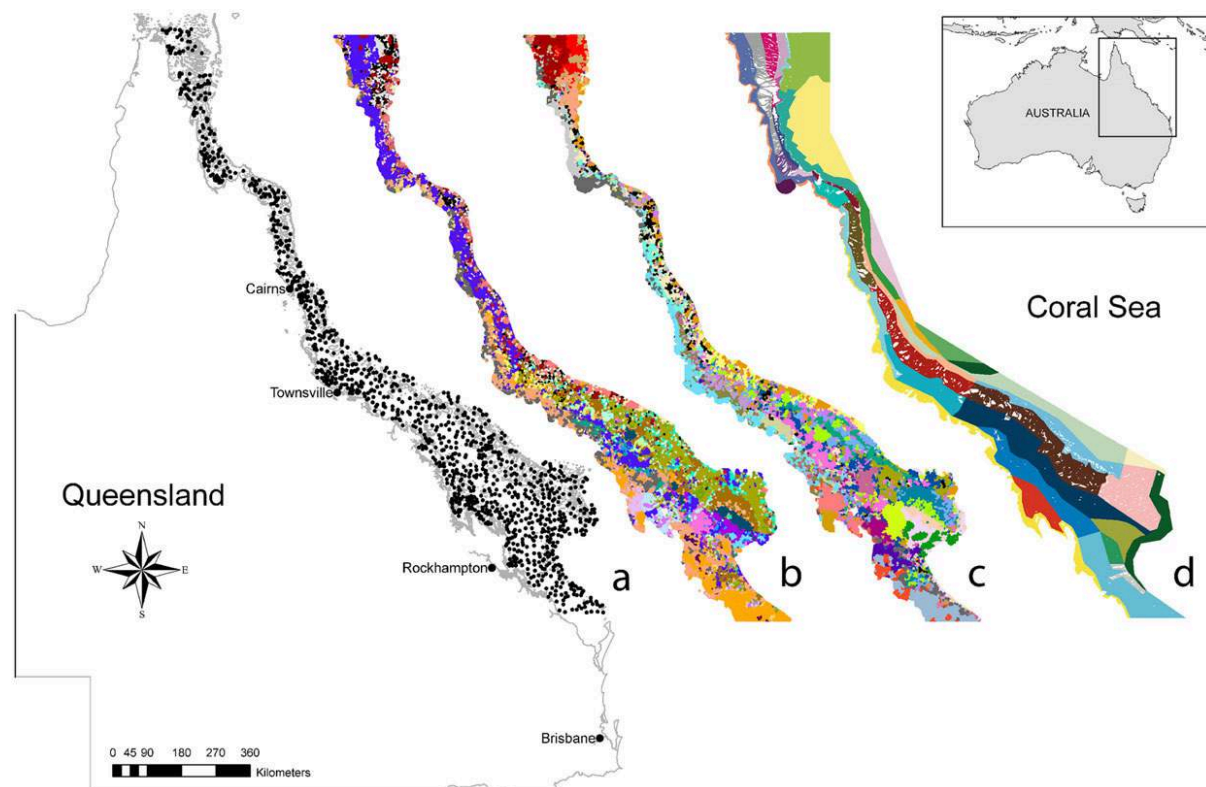


Figure 1. Great Barrier Reef, Australia: (a) sites sampled during the Great Barrier Reef Seabed Biodiversity Project (dots); (b) partitioning of the seabed region into 35 abiotic domains (each color reflects a different domain type); (c) partitioning of the seabed region into 35 weighted abiotic domains based on effect on biological responses (each color reflects a different domain type); (d) bioregions defined by the Great Barrier Reef Marine Park Authority (each color reflects a different domain type).

842 species was retained, representing 11 phyla (Table 1) across 1155 sites (Fig. 1a).

We also used predicted species distributions to evaluate the effectiveness of reserves. This allowed us to compare the use of site data and predicted data for reserve evaluation. Predicted biomass was generated for 838 species (those occurring at >23 sites) as part of the Great Barrier Reef Seabed Biodiversity Project (Pitcher et al. 2007). This was done as a 2-stage generalized linear modeling process that incorporated data from both sampling gears and a device term. First, we modeled the presence and absence of each species as a function of 28 abiotic variables. Second, the biomass response of each species to the same abiotic variables was modeled, based on the subset of sites where the species was present. Then we predicted the distribution and biomass of each species at a 0.01° resolution grid of the abiotic variables across the entire Great Barrier Reef seabed (for full details and information regarding accuracy of predictions, see Pitcher et al. [2007]).

Abiotic Data

The 28 abiotic variables used for this analysis were collated as part of the Australian Commonwealth Environ-

mental Research Facility (CERF) Marine Biodiversity Hub (www.marinehub.org) and included bathymetry, sediment composition, bottom water attributes, and satellite-derived information. A full list of variables, with source and units of measure are listed in Supporting Information. All physical variables were interpolated across a 0.01° resolution grid (Huang et al. 2010).

GBRMPA Domains

The Great Barrier Reef Marine Park Authority defined 40 non-reef bioregions based on a combination of biological and abiotic data as the first step in the Representative Areas Program to design marine reserves in the Great Barrier Reef (Fernandes et al. 2005; Kerrigan et al. 2010). However, five of these bioregions represented slope and abyssal biomes, whereas our biomes were restricted to those of the continental shelf. Thus, we examined 35 bioregions (hereafter referred to as GBRMPA domains). The number of abiotic domains and weighted abiotic domains defined in this study was set to the same as the number of GBRMPA domains on the continental shelf (35) (Fig. 1d) to provide consistency across scenarios.

To define abiotic domains, we used only those variables that are most readily available in data-poor regions.

Twelve physical variables (depth, aspect, slope, sea surface temperature [mean and seasonal range], benthic irradiance [mean and seasonal range], seabed current shear stress and sediment type; percent carbonate, gravel, sand, and mud) were used to allocate every site into 1 of 35 clusters, or domains, based on abiotic similarity. First, the range of each variable in the region was re-scaled between zero and one to standardize different units of measurement. These standardized physical variables were then clustered to define abiotic domains with the function *clara* in the package *cluster* (Kaufman & Rousseeuw 1990) in the R statistical computing environment (R Development Core Team 2009). The function *clara* samples several subsets of the data and assigns the remaining objects to the best cluster solution, enabling the analysis of very large data sets. We used a sample size of 17,000 and set the number of repetitions to 10 to ensure adequate representation of the data set. A full description of the algorithm is in Kaufman and Rousseeuw (1990). The number of clusters was set at 35 abiotic domains (Fig. 1b) to coincide with the number of bioregions used in the zoning of the Great Barrier Reef (see above).

Some variables, such as sediment type, have a greater influence on biological composition than other variables, such as slope and aspect (Pitcher et al. 2007; Ellis et al. 2012; Pitcher et al. 2012). Furthermore, the relationship between compositional change and abiotic gradients typically is non-linear and may include threshold changes (Pitcher et al. 2012). These factors were taken into account by using the abiotic data set of Pitcher et al. (2012) in which each of the same 28 variables for the region were transformed and weighted by the non-linear composition–environment relationships and the conditional importance of variables and estimated with the R package *gradientForest* (Ellis et al. 2012). Thus, all variables were available on a common biological influence scale. We grouped this transformed and weighted abiotic data set into 35 groups as described for the abiotic domains (Fig. 1c) to provide a set of biologically informed abiotic domains.

Reserve Design Parameters

Target-based reserve design seeks to conserve a fixed percentage of each conservation feature in a clumped fashion for minimal impact on commercial and recreational users of a region (Carwardine et al. 2009). Clumping refers to the design of reserves whereby adjacent planning units are preferentially selected for inclusion in a reserve which aids management. For each of the 3 kinds of surrogate domains (abiotic domains, weighted abiotic domains, and GBRMPA domains), 30% of each domain was selected as a target in the reserve design software *Marxan* (Ball & Possingham 2000; Possingham et al. 2000; Watts et al. 2009). *Marxan* finds optimal solu-

tions to target-based conservation problems with variable cost and clumping. In this case, we included scenarios that were clumped and scenarios that had no clumping constraints (Fig. 2) in order to quantify differences in conservation outcomes.

Reserve system design in the real world also accounts for costs (Ando et al. 1998; Carwardine et al. 2009). We included a cost value that represented the relative amount of commercial fishing effort in each unit, which could be affected if reserves were to be selected in areas where fishing occurs. The fishery data we used were fishing effort for the Queensland East Coast Otter Trawl Fishery, which target prawns (shrimps), scallops, and several other permitted species; it is the largest Queensland fishery in terms of catch and value (Department of Primary Industries and Fisheries 2006). The fishing effort data used were total annual hours trawled per 0.01° grid cell, averaged over 9 years (1996–2004) and weighted so that the contribution of more recent trawling was greatest (Pitcher et al. 2007). The data were subsequently normalized to sum to one to obtain a relative value for cost for each planning unit.

Assessing Reserve Design for Conservation

To define the reserve design problem, we considered four scenarios for each kind of surrogate domain. First, we designed a reserve system with no clumping (i.e., no penalty for scattered reserve design) and no consideration of the cost to fisheries if reserves are placed in a location of high fishing value. While this is impractical, it provides a starting point for comparison. Second, we designed a system in which reserves were more clumped, to better reflect management requirements, but fishing cost was not considered. We used a total reserve boundary length of 95 decimal degrees ($\pm 5\%$) for all clumped scenarios to ensure comparability between scenarios. This boundary length was chosen because it produced reserves that were not too scattered and unenforceable or too large and impractical under all scenarios. Third, we accounted for fishing cost but ignored clumping. Fourth, we accounted for both fishing cost and clumping (Fig. 2).

Finally, to allow comparison to a random scenario, we also created reserves by treating the entire region as a single large domain, setting the reserve target as 30% of the entire area. All four scenarios (cost and no clumping, cost and clumping, no cost and no clumping, and no cost and clumping) were analyzed for this random scenario.

All reserves were designed using *Marxan*, and we repeated the reserve design process 100 times for each scenario (10,000,000,000 iterations for each run) (Ball & Possingham 2000). The results of the best solution from this process are reported here for each of the 4 scenarios and for each surrogate domain. The best scenario was chosen based on an objective function that combined the cost of a reserve system, a penalty for any ecological

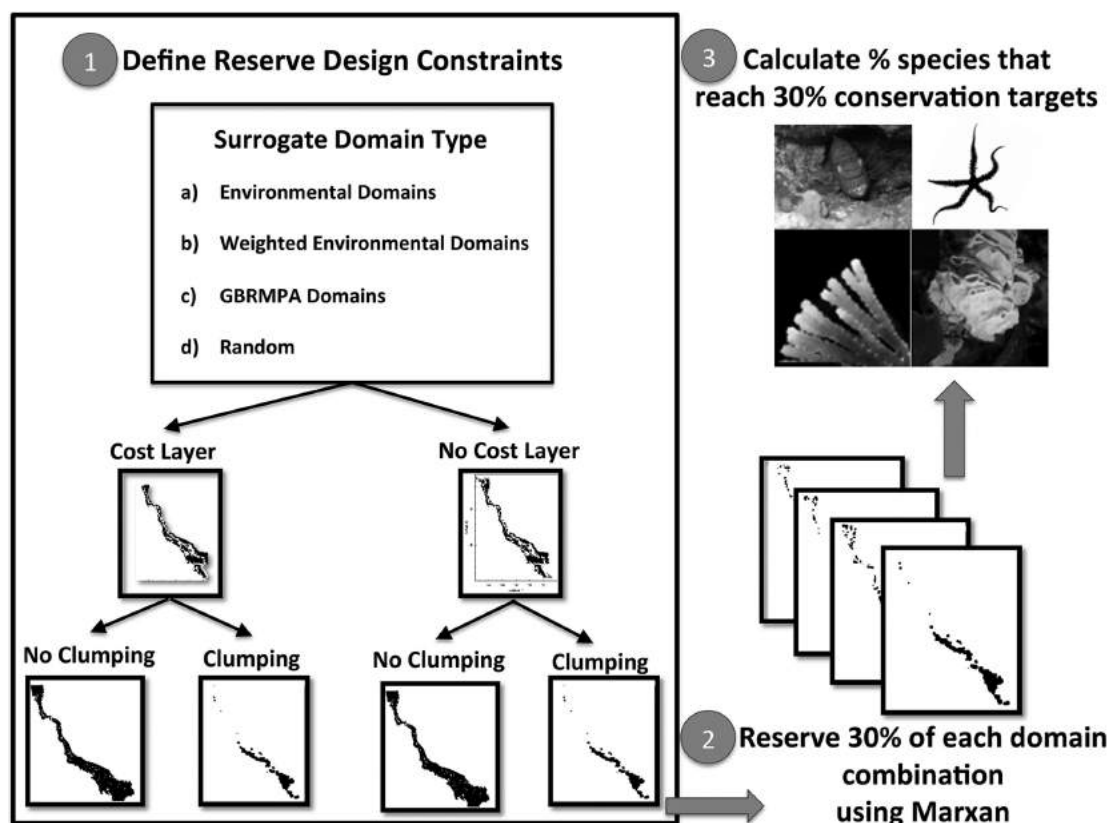


Figure 2. Stages in the assessment of conservation plans designed using surrogates: (1) reserve design, (2) reserve selection, and (3) performance assessment (GBRMPA, Great Barrier Reef Marine Protected Area).

targets that are not met, and a penalty for the amount of clumping of the reserve (Possingham et al. 2000).

Our results are 16 scenarios that are efficient reserve systems designed based on the intersection of four kinds of surrogate domains (including random) and four combinations of cost and clumping constraints. For the reserve produced in each scenario, we calculated the percentage of species reaching different conservation targets as a measure of success of the reserve. Representativeness was tested on collected data and predicted distributions. Conservation targets were set at 30% of the biomass of each species. To compare the number of species that missed the conservation target and the amount by which the target was missed, we calculated the mean percentage gap for each scenario:

$$\sum_{i=1}^N \frac{\left(\frac{P_i}{0.3}\right)}{N} \times 100, \quad (1)$$

where P_i is the amount that species i is less than the 30% conservation target and N is the total number of species.

Results

Using data for species at each of the 1189 sites sampled by the epibenthic sled, the percentage of species

reaching the conservation target ranged between 32% and 46% across all scenarios with the highest level of protection provided by abiotic domains (Table 2). The number of species that missed their conservation target and the amount by which they missed their target was represented as the mean percentage gap for each scenario. Based on site inventory data, the mean percentage gap was 54–100% across all scenarios; the best protection was provided by GBRMPA domains (Table 2; Fig. 3a).

Based on predicted data, the percentage of species reaching the conservation target was 9–68% across all scenarios. The conservation target was achieved for the highest proportion of species through either the abiotic domains or GBRMPA domains scenarios. The mean percentage gap for each scenario ranged between <1% and 14% but was $\leq 6\%$ for all scenarios except random reserves (Table 2; Fig. 3b).

When species were ordered by the level of protection, the curve that depicted the percentage biomass conserved for each species as assessed by site collection data showed a gradual increase in protection (Fig. 3a). In contrast, the results for predicted distributions showed sharp changes in the percentage biomass conserved at each end of the range; the majority of species were closer to the conservation target (Fig. 3b).

Table 2. Percentage of species reaching the conservation target and the mean percentage gap^a for each of 4 reserve selection strategies, as assessed using site data (epibenthic sleds at 1189 sites) and modeled biomass (predicted across all sites in the study area).

Criterion ^a	Assessment basis	Constraints ^b	Selection			
			abiotic domains	strategy weighted abiotic domains	GBRMPA ^c domains	random reserves
Percent reaching target	site data	none	51	41	45	46
Percent reaching target	site data	cost	32	45	45	31
Percent reaching target	site data	clumping	50	35	35	36
Percent reaching target	site data	both	36	46	46	33
Percent gap	site data	none	54	60	56	60
Percent gap	site data	cost	87	80	60	100
Percent gap	site data	clumping	54	62	73	86
Percent gap	site data	both	84	65	58	96
Percent reaching target	modeled biomass	none	41	9	50	41
Percent reaching target	modeled biomass	cost	60	55	68	61
Percent reaching target	modeled biomass	clumping	54	46	51	35
Percent reaching target	modeled biomass	both	65	59	61	61
Percent gap	modeled biomass	none	0.2	1	0.1	0.3
Percent gap	modeled biomass	cost	6	5	3	10
Percent gap	modeled biomass	clumping	5	5	3	14
Percent gap	modeled biomass	both	6	4	4	10

^aConservation target set at 30% of the total biomass, and percent gap refers to the number of species that missed the conservation target.

^bOpportunity cost to commercial fisheries and clumping cells to produce a compact and more manageable reserve. These constraints were considered individually and in combination.

^cGreat Barrier Reef Marine Protected Area.

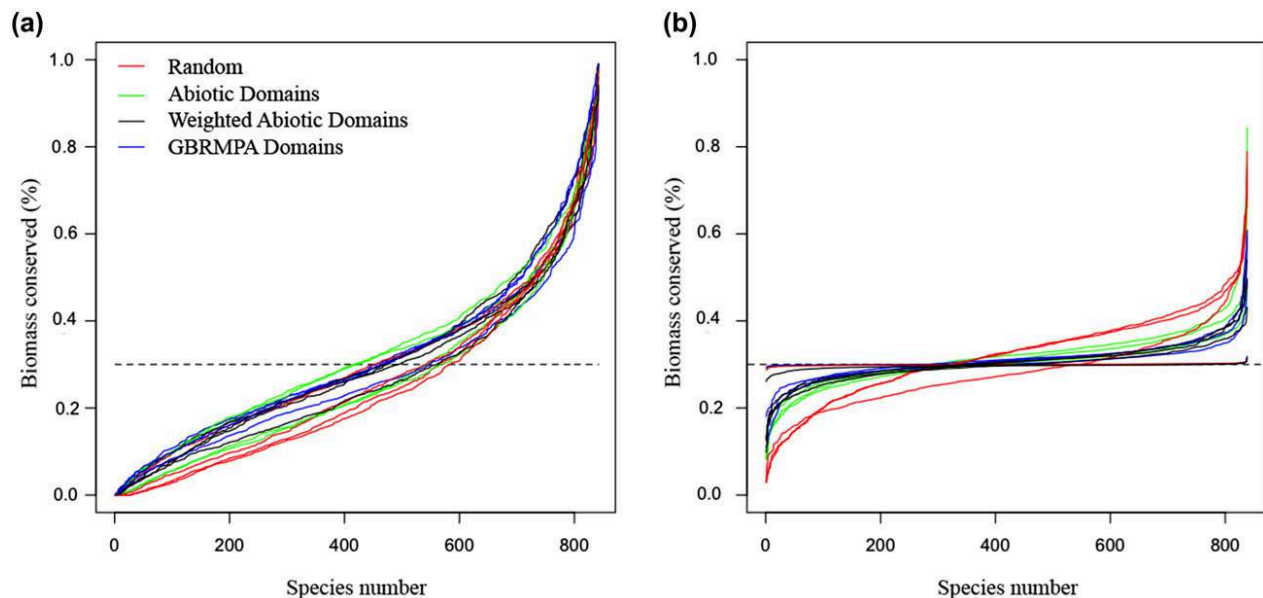


Figure 3. Percent biomass conserved for each of the 842 species representing 11 phyla, ordered by proportion of biomass conserved when reserves are evaluated using (a) actual biomass data on 842 species and (b) predicted biomass for 838 species. Each of the 4 scenarios representing different approaches to surrogacy are depicted (red, random; green, abiotic domains; black, weighted abiotic domains; and blue, Great Barrier Reef Marine Protected Area [GBRMPA] domains) as are results of each of the 4 constraint combinations (clumping constraints only; cost constraints only; clumping and cost constraints; no constraints) shown for each scenario (dotted line, 30% conservation target).

To compare the effect of constraints, we used the results of the predicted species analyses because similar trends were reflected when the site data were used. No cost and no clumping constraints resulted in the most

efficient representation (Fig. 4a). The mean percentage gap was negligible, <1–2% across all surrogate domains when no cost and no clumping was considered. This increased to 3–10% when cost constraints were considered

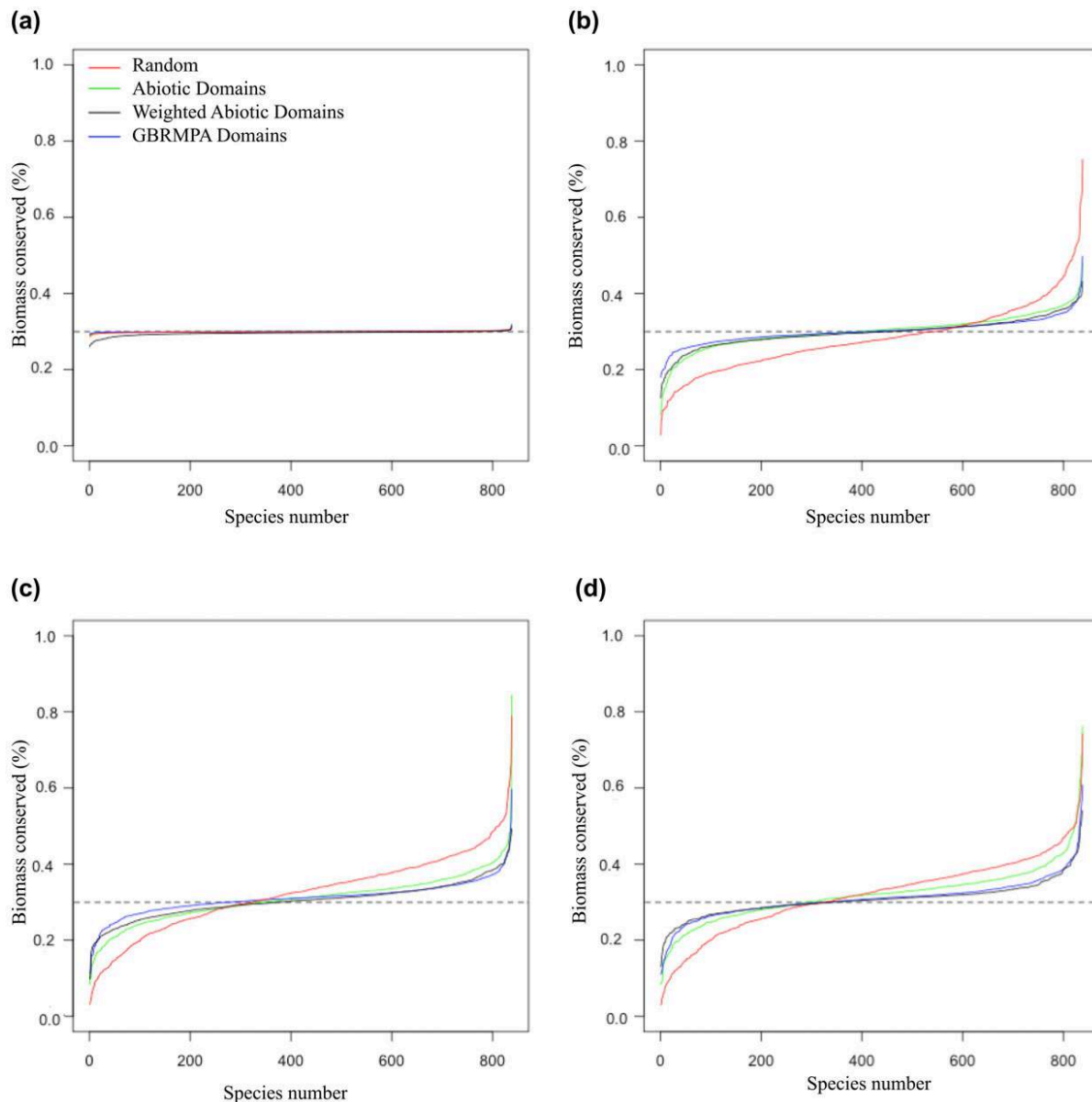


Figure 4. Summary of the effect of each of the reserve-design cost and clumping constraint combinations—(a) no cost and no clumping (compactness of reserve), (b) cost and no clumping, (c) no cost and clumping, (d) cost and clumping—on each result of the 4 domain scenarios (red, random site selection; green, abiotic domains; black, weighted abiotic domains; blue, Great Barrier Reef Marine Protected Area [GBRMPA] domains; dashed line, 30% conservation target). Species are ordered by the proportion of biomass conserved for each of the 838 species predicted to occur across the Great Barrier Reef based on 2-stage species distribution modeling.

(Fig. 4b) and to 3–14% when clumping constraints were considered (Fig. 4c). When both cost and clumping constraints were considered, however, there was little difference in the total area under the conservation target compared to the constraints considered individually (Fig. 4d), and the mean percentage gap was 4–10%.

When both cost and clumping constraints were applied, fewer species were severely under-represented using the weighted abiotic domain and GBRMPA domains compared to the abiotic domain and random scenarios

(e.g. Fig. 4d), regardless of whether effectiveness was evaluated using site inventory data or predicted biomass. In all scenarios where cost was not considered, the proportions of species conserved did not differ substantially across domain approaches and were similar to the proportions of species biomass conserved using the random approach (e.g. Fig. 4a & c). Similarly, the proportion of species that was substantially under-represented was consistently low across approaches when no cost or clumping was considered; however, the mean

percentage gap only remained consistently low across all scenarios, including those that incorporated cost, for weighted abiotic domains and GBRMPA domains (Fig. 4).

Discussion

We found that reserve systems designed using abiotic surrogates were substantially better than a random reserve system and performed similarly to GBRMPA domains. When we designed abiotic domains without any biological knowledge, however, the representation of species was less equitable (i.e. largely over- or under-represented) across all species relative to the level of representation achieved using other domains (Fig. 3). Previous studies have suggested that abiotic surrogates can assist in reserve design (e.g., Beger & Possingham 2008). We found that abiotic domains may be used for an initial reserve design when biological information is lacking, but domains that are biologically informed, either through weighting the biological importance of the abiotic data or by incorporating biological data explicitly, will produce much more effective reserves. This supports the use of biological data in development of regionalizations for conservation (e.g., Coops et al. 2009; Leathwick et al. 2011; Terauds et al. 2012).

Although it is relatively straightforward to collect relevant biological data for a specific species or taxon, collecting biological information for all of biodiversity is much more difficult and time consuming and virtually impossible at large scales. One way to reduce these costs may be to collect comprehensive biological and corresponding abiotic data for a subset of sites and extrapolate across the region. This will provide more taxonomically comprehensive information to develop biologically informed abiotic domains across an entire region, which could subsequently be used to aid conservation planning. Abiotic surrogates have successfully predicted biodiversity patterns (e.g., Carmel & Stoller-Cavari 2006), and species distributions and assemblages (Guisan & Zimmermann 2000; Ferrier et al. 2007; Pitcher et al. 2012). The success with using abiotic variables to explain and predict these patterns may explain the improvement in representation found during this study for abiotic domains that incorporate biological information (weighted abiotic domains). We suggest that the use of weighted abiotic variables may be a cost-effective approach to representative reserve design, if a greater proportion of the region of interest can be conserved.

Contrary to the opinion that the use of site data is preferable to predicted data for evaluating a surrogate (Rodrigues & Brooks 2007), the use of site data for evaluation does not necessarily provide a true reflection of the effectiveness of reserves (Fig. 3). The proportion of species conserved using the predicted distributions shows an expected distribution for a reserve

system that is working reasonably well, with some species slightly under-represented and some species slightly over-represented, but few species at either end of that spectrum (Fig. 3b). Using site data, however, many species were severely under-represented, with the proportion of species conserved gradually increasing (Fig. 3a). Although neither approach of evaluation is entirely correct, using data collected at sites will likely underestimate the proportion of each species conserved when sampling density is low. Conversely, there can be large uncertainty in the modeling and prediction of species distributions and overestimation of the proportion of each species conserved is likely. It is therefore also important that prediction uncertainty is explicitly considered when designing reserves. One way to mitigate the uncertainty of predictions may be to increase the conservation targets to increase the probability that the species will be adequately captured within the reserve system (Game et al. 2008; Tulloch et al. 2013).

We suggest that the cost of collecting biological data will be less than the potential social costs and the cost incurred to commercial ventures if reserves are placed in areas of high commercial value and that the cost effective option of gathering sufficient data to weight abiotic variables within a landscape is a reasonable trade-off between commercial and biodiversity values for a region. We strongly support the inclusion of stakeholders in the reserve design process, to clarify that approaches that are more financially viable will not necessarily provide satisfactory outcomes for biodiversity conservation. This will assist discussions that are more likely to lead to reserve systems that maximize overall efficacy of reserve implementation and sustainability without compromising biodiversity conservation.

In summary, abiotic surrogates can assist conservation planning, with substantial improvements in performance achieved when they are biologically informed. The collection of biological data is essential to the design of comprehensive and representative reserve systems. The relationships between biota and the environment have been studied for many ecosystems (e.g., trees in Guisan et al. [1998]; freshwater fish and aquatic insects in Santoul et al. [2005]; marine seabed systems in Pitcher et al. [2012]; birds in Patten & Smith-Patten [2012]). Although this knowledge should continue to be used to inform large-scale reserve design, they should be applied with caution due to the potential for taxonomic bias.

This is the first comprehensive study of reserve design performance for seabed systems, and use of our methods may produce different results in other ecosystems. It will be important to ensure that reserve designs include information for all parts of an ecosystem, such as the inter-reef seabed or fringing forest shrubland, as well as the recognized major habitats, such as coral reefs or forests, to ensure representative conservation efforts.

Supporting Information

A list of variables used and their sources and units of measurement (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.

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Appendix S1. List of variables used, with their sources and units of measurement.

Variable	Measurement Unit	Source
Depth	meters	GBRMPA
Aspect	degrees	Derived from depth
Slope	degrees	Derived from depth
Seabed current shear stress	Pascals	James Cook University
Carbonate	percentage	Geosciences Australia (MARS)
Gravel	percentage	Geosciences Australia (MARS)
Sand	percentage	Geosciences Australia (MARS)
Mud	percentage	Geosciences Australia (MARS)
Sea Surface Temperature (average and seasonal range)	degrees Celsius	MODIS Terra
Benthic irradiance (average and seasonal range)	-	Derived from depth, K490, latitude
Chlorophyll-a (average and seasonal range)	mg/m ³	SeaWiFS
Light attenuation, K490 (average and seasonal range)	m ⁻¹	SeaWiFS
Bottom Water Temperature (average and seasonal range)	degrees Celsius	CSIRO (CARS2006)
Bottom Water Nitrate (average and seasonal range)	micromole / L	CSIRO (CARS2006)
Bottom Water Oxygen (average and seasonal range)	ml / L	CSIRO (CARS2006)
Bottom Water Phosphate (average and seasonal range)	micromole / L	CSIRO (CARS2006)
Bottom Water Salinity (average and seasonal range)	PSU	CSIRO (CARS2006)
Bottom Water Silicate (average and seasonal range)	micromole / L	CSIRO (CARS2006)



A review of selection-based tests of abiotic surrogates for species representation

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Abstract: *Because conservation planners typically lack data on where species occur, environmental surrogates—including geophysical settings and climate types—have been used to prioritize sites within a planning area. We reviewed 622 evaluations of the effectiveness of abiotic surrogates in representing species in 19 study areas. Sites selected using abiotic surrogates represented more species than an equal number of randomly selected sites in 43% of tests (55% for plants) and on average improved on random selection of sites by about 8% (21% for plants). Environmental diversity (ED) (42% median improvement on random selection) and biotically informed clusters showed promising results and merit additional testing. We suggest 4 ways to improve performance of abiotic surrogates. First, analysts should consider a broad spectrum of candidate variables to define surrogates, including rarely used variables related to geographic separation, distance from coast, hydrology, and within-site abiotic diversity. Second, abiotic surrogates should be defined at fine thematic resolution. Third, sites (the landscape units prioritized within a planning area) should be small enough to ensure that surrogates reflect species' environments and to produce prioritizations that match the spatial resolution of conservation decisions. Fourth, if species inventories are available for some planning units, planners should define surrogates based on the abiotic variables that most influence species turnover in the planning area. Although species inventories increase the cost of using abiotic surrogates, a modest number of inventories could provide the data needed to select variables and evaluate surrogates. Additional tests of nonclimate abiotic surrogates are needed to evaluate the utility of conserving nature's stage as a strategy for conservation planning in the face of climate change.*

Keywords: conservation planning, conserving nature's stage, geodiversity, incidental representation, surrogacy tests

Una Revisión de Pruebas Basadas en Selección de los Sustitutos Abióticos para la Representación de las Especies

Resumen: *Ya que quienes planean la conservación carecen comúnmente de la información sobre dónde se presentan las especies, los sustitutos ambientales—incluidos las condiciones geofísicas y los tipos de clima—se han utilizado para priorizar sitios dentro de un área de planeación. Revisamos 622 evaluaciones de la efectividad de los sustitutos abióticos que representaban a 19 especies en las áreas de estudio. Los sitios seleccionados usando sustitutos abióticos representaron más especies que un número igual de sitios seleccionados al azar en 43% de las pruebas (55% para las plantas) y en promedio, mejoraron la selección al azar de sitios en un 8% (21% para las plantas). La diversidad ambiental (DA) (42% de mejoramiento promedio en la selección al azar) y los agrupamientos de información biótica mostraron resultados prometedores y merecen pruebas adicionales. Sugerimos cuatro formas para mejorar el desempeño de los sustitutos abióticos. Primero, los analistas deberían considerar un espectro amplio de las variables candidatas para definir a los sustitutos,*

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incluidas las variables que rara vez se usan relacionadas con la separación geográfica, la distancia desde la costa, la hidrología y la diversidad abiótica dentro del sitio. Segundo, los sustitutos abióticos deberían ser definidos en una resolución temática refinada. Tercero, los sitios (las unidades de paisaje priorizadas dentro de un área de planeación) deberían ser lo suficientemente pequeños para asegurar que los sustitutos reflejen el ambiente de las especies y para producir priorizaciones que equivalgan a la resolución espacial de las decisiones de conservación. Cuarto, si los inventarios de especies están disponibles para algunas unidades de planeación, quienes planean deberían definir a los sustitutos con base en las variables abióticas que más influyan sobre el volumen de especies en el área de planeación. Aunque los inventarios de especies incrementan el costo de usar sustitutos abióticos, un número modesto de inventarios podría proporcionar los datos necesarios para seleccionar a las variables y evaluar a los sustitutos. Se necesitan pruebas adicionales de sustitutos abióticos no-climáticos para evaluar la utilidad de conservar el estado de la naturaleza como una estrategia para la planeación de la conservación de frente al cambio climático.

Palabras Clave: conservar el estado de la naturaleza, geodiversidad, planeación de la conservación, pruebas de sustitución, representación secundaria

Introduction

Because conservation planners typically lack data on where species occur, surrogates are often used to prioritize sites for conservation. One class of surrogates—geophysical surrogates defined by enduring features such as elevation, insolation, and soil properties—has been proposed to prioritize sites in the face of climate change (Hunter et al. 1988). We refer to this coarse-filter strategy as *conserving nature's stage*. The idea is that sites that collectively represent geodiversity should also represent many biodiversity targets regardless of climate.

To test this idea, we set out to review studies testing how well geodiversity (nonclimate surrogates) represented species. We expanded our review to consider all types of abiotic surrogates because surrogates were defined partially by climate variables in 12 of the 14 studies we found. To the extent that climate diversity in a planning area is related to enduring geographic features (e.g., elevation, aspect, cold air pooling, and location with respect to prevailing winds), such climate diversity is a function of geodiversity, and sites with high climate diversity today should have high climate diversity in the future. Thus, all 14 studies reflect the influence of geodiversity, although not as directly as we would have preferred.

Abiotic conditions are associated with species richness and species turnover (Lawler et al. 2015). However, such findings do not prove that sites selected to represent diversity in those conditions can be used as abiotic surrogates to represent species. For example, Shokri and Gladstone (2013) reported that although their (biotic) surrogates were strongly associated with species turnover, the surrogates did not identify sites that represented species efficiently. Thus, although congruence between abiotic variables and species turnover justifies attempts to develop surrogates, eventually surrogates must be evaluated by selection-based tests. A selection-based test uses a site prioritization algorithm (Pressey et al. 1993; Margules & Pressey 2000) to select

complementary sites that represent the surrogates and then evaluates how well these sites represent species.

Although dozens of studies have evaluated cross-taxon and biotic surrogates (Rodrigues & Brooks 2007; Lewandowski et al. 2010; Mellin et al. 2011), fewer studies have evaluated abiotic surrogates. Rodrigues and Brooks (2007) reported that cross-taxon and biotic surrogates (36 studies, 419 tests) outperformed abiotic surrogates (4 studies, 163 tests). Here, we present the first review to focus solely on abiotic surrogates. Our goals were to evaluate how well sites prioritized to represent abiotic surrogates also represented species, identify conditions under which abiotic surrogates are effective, and suggest how to devise more effective abiotic surrogates.

We summarized evidence from all available studies that quantified how well sites prioritized to represent abiotic surrogates also represented species. In addition, we investigated whether surrogate performance was affected by 4 factors: choice of abiotic variables; statistical procedure used to define multivariate abiotic space; thematic resolution (degree to which fine gradations of abiotic variables are recognized); and size of sites (units of selection within the study area). We expected surrogate success would increase if the surrogate was defined using abiotic variables associated with species turnover and surrogate performance to be worst for statistical procedures that used arbitrary bins and ignored within-bin and between-bin heterogeneity. We expected surrogate performance to increase with thematic resolution up to an asymptote of diminishing marginal improvement. We expected that as sites become larger, the values of abiotic variables in the site might not reflect the abiotic conditions experienced by species in the site, thereby leading to poor surrogate performance. Finally, in light of the evidence related to these questions, we devised recommendations on how conservation biologists should conduct future surrogacy tests and use abiotic surrogates in systematic conservation planning.

Methods

In January 2014, we searched Google Scholar and Web of Science for publications that included the terms “surroga*” and “conservation.” We retained studies that selected a subset or subsets of sites (planning units) to represent abiotic diversity (the surrogate) and evaluated surrogate performance with species accumulation index (SAI) or correlation of irreplaceability scores (CIS). The SAI (Ferrier & Watson 1997; Rodrigues & Brooks 2007) starts with a set of sites (planning units), each of which has been surveyed for species within a broad taxonomic group. Sites are selected to represent the surrogates, ignoring the survey data. Then the survey data are consulted to calculate the number of species represented in the selected sites, plotting the species represented against number of sites selected as a species accumulation curve. This curve is compared with a random curve derived by selecting the same number of randomly selected sites and to an optimum curve derived by using the survey data to select sites that maximize the cumulative number of species represented. The SAI is given by $(S - R)/(O - R)$, where S is the area under the surrogate curve, R is the area under the random curve, and O is the area under the optimum curve (Fig. 1). CIS (Pressey et al. 1994) is the Spearman correlation coefficient (R^2) between planning unit ranks (irreplaceability scores) for representing surrogate diversity and the ranks of the same units for representing species.

We extracted SAI values based on the full species accumulation curves (Fig. 1) when possible. For studies that reported target representation only for specific fractions of the landscape, we selected the point estimate of SAI at 15% of sites selected or at the proportion closest to 15% (Fig. 1). If a study did not report the optimum, we assumed the optimum was 100% for all landscape fractions $\geq 15\%$. This was reasonable because most of the reported optimum values were well over 90%. In cases where the unknown optimum was $<100\%$, our use of 100% yielded a low (conservative) estimate of SAI. Following Rodrigues and Brooks (2007), we considered an SAI test to have a positive (better than random) result, when $SAI > 0.10$; a negative result, when $SAI < -0.10$; and a null result otherwise (approximately the same as random). Several papers reported variants of SAI. We converted these to SAI values as described in Supporting Information.

For tests reporting CIS, we considered a surrogacy test to have a positive result when $R^2 > 0.30$ and a negative result when $R^2 < -0.30$ because absolute values of most CIS scores were <0.20 , and the largest value was 0.47.

Several studies measured effectiveness as the investigator systematically varied the size of planning units, number or types of abiotic variables used to define diversity, the selection algorithm, or some other factor (Table 1: last column). We report the main patterns within and across studies.

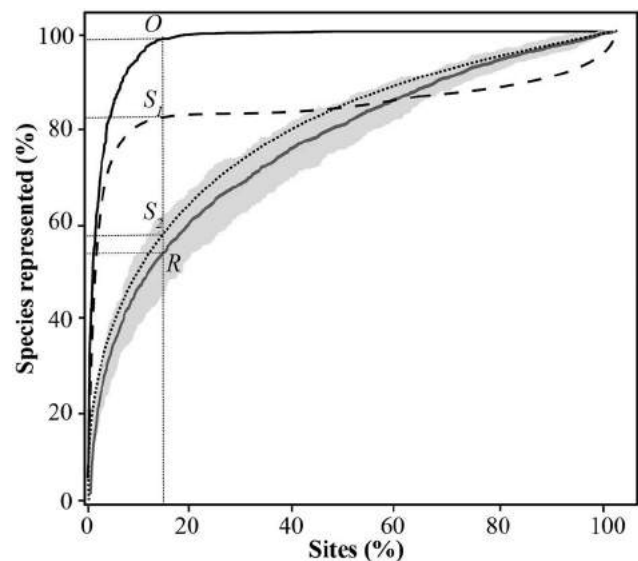


Figure 1. An illustration of how the species accumulation index (SAI) is calculated. The $SAI = (S - R)/(O - R)$, where S is the area under the curve indicating the average percentage of target species represented when selecting conservation areas based on surrogate data (dashed line, surrogate 1; dotted line, surrogate 2); R is the area under a curve indicating the average percent of species represented when sites are selected randomly (lower solid gray line with a gray band indicating 95% CI); and O is the area under the optimum curve indicating the largest number of species that can be represented in a given number of sites (upper solid line). The SAI can also be calculated at a particular point, such as at 15% of total area in this illustration. For surrogate 1 (S_1), SAI is 0.32 for the full curve, 0.57 at 15% of total area, and SAI_{95} is 0.55. For surrogate 2, SAI is 0.07 for the full curve and for the point estimate at 15% of total area, and SAI_{95} is negative 0.08.

Results

We identified 14 studies that addressed effectiveness of abiotic surrogates in 19 study areas and reported 622 tests of abiotic surrogates (Table 1). Over one-third of the 622 tests were from northeastern New South Wales, Australia. Of the 19 study areas, 12 were in temperate zones, 6 were in tropical zones, and 1 spanned temperate and arctic zones; 15, 3, and 1 study areas were in terrestrial, marine, and freshwater systems, respectively. The size of the study region varied from 418 km² to 21 million km².

Of the 622 tests of abiotic surrogates, surrogates performed better than random in 265 cases (43%), about the same as random in 266 cases (43%), and worse than random in 91 cases (15%) (Table 1). Although positive results outnumbered negative results, positive results did not exceed 50% in any realm (terrestrial, marine, or freshwater).

Table 1. Studies that quantified how well abiotic surrogates represented biotic diversity in a reserve-selection framework.^a

Citation	Realm, climate zone ^b	Study area	Size of study area (km ²)	Number and size of sites; units of selection	Outcome of surrogacy tests			Taxon or feature used to evaluate the surrogate (separate test for each)	Numbers of each type of abiotic variable ^c	Focal covariates ^d
					+	0	-			
Araujo et al. 2001	terr., temp.	W Europe	5,200,000	2089 grid cells; 2500 km ²	4	2	0	plants, birds, mammals, reptiles, amphibians, all species, endemic vertebrates	1 topographic, 2 energy, 3 climate	test taxon
Beier & Albuquerique 2015	terr., temp.	W Europe	5,200,000	2195 grid cells; 2500 km ²	4	0	1	amphibians, reptiles, birds, mammals, all vertebrates	4 topographic, 20 climate, 8 energy, 5 productivity	test taxon (within Europe), and study areas (4)
	terr., temp.	Arizona	295,000	1317 inventory cells; 6 km ²	1	0	0	birds		
	terr., temp.	Spain	506,000	4301 cells; 100 km ²	1	0	0	birds		
	terr., trop.	Zimbabwe	391,000	360 cells; 625 km ²	1	0	0	plants		
Bonn & Gaston 2005	terr., temp.	South Africa and Lesotho	1,256,000	1858 grid cells; 676 km ²	2	2	0	bird presence, bird abundance, vegetation types (2 levels of coverage)	4 topographic, 2 energy, 8 climate, 3 productivity	test taxon
Dalleau et al. 2010	mar., trop.	coral reefs of Wallis Island	300	41 circles of 5 sizes (0.0078 to 0.785 km ²)	48	0	0	algae, invertebrates, commercial fish, all fish, corals	3 topographic (depth, slope, landform), 1 geol (substrate)	test taxon, number of surrogate classes, size of site
Ferrier & Watson 1997	terr., temp.	NE New South Wales	82,000	198 grid cells; 2 sizes (25 and 0.04 km ²)	51	144	13	ants, beetles, spiders, reptiles, birds, bats, rainforest trees, rainforest understorey plants, open forest trees, open forest understorey plants	A: 2 climate, 1 soil (fertility), 1 topog (ruggedness) B: 12 climate, 4 energy, 1 topog, 1 soil C: 12 climate, 4 energy, 4 topographic, 3 soil	method of defining abiotic diversity (clustering, overlay, ED), thematic resolution, site size, variables used to define abiotic diversity effect of using biotic data to weight variables

Continued

Table 1. Continued.

Citation	Realm, climate zone ^b	Study area	Size of study area (km ²)	Number and size of sites; units of selection	Outcome of surrogacy tests			Taxon or feature used to evaluate the surrogate (separate test for each)	Numbers of each type of abiotic variable ^c	Focal covariates ^d
					+	0	-			
Grantham et al. 2010	terr., temp.	upper NE New South Wales	37,000	6712 forest stands; mean 2 km ²	6	24	0	mammals, birds, reptiles, frogs, plants, all taxa	2 climate, 1 soil (fertility), 1 topographic (slope)	study areas (2), test taxon, response variables (SAI variants, correlation of irreplacability scores)
	terr., temp.	lower NE New South Wales	45,000	7021 forest stands; mean 2 km ²	18	11	1			
Hortal et al. 2009	terr., temp.	W Europe	5,200,000	2289 grid cells; 2500 km ²	0	0	2	amphibians and reptiles	6 climate	discrete versus continuous <i>p</i> median
Januchowski-Hartley et al. 2011	terr., temp.	Iberian peninsula	625,000	251 grid cells; 2500 km ²	2	0	0			
	freshwater, trop.	Queensland	11,862	7210 stream reaches; mean 1.6 km	0	12 ^e	0	fishes	6 climate	clustering algorithms (<i>n</i> = 3), number of clusters (2, 4, 6, or 8), and effect of using biotic data to weight variables
Sarkar et al. 2005	terr., temp.	Québec	324,000	3890 grid cells; 83.3 km ²	2	0	2	at-risk plants and vertebrates	4 climate, 3 topographic, 1 soil	number of surrogates (56, 51, 42, or 32)
	terr., trop.	Queensland	29,600	251 grid cells; 118 km ²	4	0	0	plants		number of surrogates (54, 49, 40, or 30)
Schloss et al. 2011	terr., temp.	Columbia Plateau of United States	112,000	1200 watersheds; mean 93 km ² , S.D. 36 km ²	1	0	0	vegetation types	2 topographic, 3 geologic, 4 climate	-

Continued

Table 1. Continued.

Citation	Realm, climate zone ^b	Study area	Size of study area (km ²)	Number and size of sites; units of selection	Outcome of surrogacy tests			Taxon or feature used to evaluate the surrogate (separate test for each)	Numbers of each type of abiotic variable ^c	Focal covariates ^d
					+	0	-			
Sutcliffe et al. 2015	mar., trop.	Great Barrier Reef	348,000	grid cells; ~1 km ²	7	7	2	840 species in 11 phyla	4 climate, 5 topographic, 11 geology, substrate (including 7 related to water chemistry), 1 energy	effect of using biotic data to weight variables, effect of cost and connectivity constraints, type of biotic test data (SDM, inventory)
Trakhtenbrot & Kadmon 2005, 2006	terr., temp.	Israel	28,000	726 grid cells; 25 km ²	52	10	0	native plants, range-restricted plants	4 climate, 13 geologic (percentage of each of 13 lithologic units)	test feature (all plants, rare plants), clustering algorithm ($n = 6$), variable weighting scheme
van Wijnberg et al. 2012 ^f	mar., trop.	New Caledonia	418	27 circles of 9 sizes (0.0009 to 25 km ²)	61	52	70	fishes (raw species number, rarity-weighted species number, evenness-weighted diversity)	7 geomorphologic classifications	ways of measuring test feature ($n = 3$), size of selection unit, thematic resolution of abiotic bins, and number of selection units (22–27)
Williams et al. 2012	terr., temp., and Arctic	North America	21,000,000	88 polygons varying from ~10 ³ to 10 ⁶ km ²	0	2	0	pollen types	A: 8 climate B: 2 geographic (latitude, longitude), 1 topographic (mean elevation)	independent variables (climate vs. geography)

^aCorrelation of irreplaceability scores was used in 12 tests by Grantham et al. (2010) and both tests by Williams et al. (2012); all other tests involved species accumulation index (SAI).

^bAbbreviations: terr., terrestrial; mar., marine; temp., temperate; trop., tropical.

^cEnergy variables included potential evapotranspiration and insolation. Soil and substrate variables included geologic substrate and soil and water chemistry. Plant productivity variables included normalized difference vegetation index and net primary productivity.

^dAbbreviations: ED, environmental diversity; SAI, species accumulation index; SDM, species distribution models.

^eThis paper reported that no surrogate performed better than R₀₅ but did not report R or R₀₅, so we could not convert to an SAI-like index. We accepted the authors' interpretation of "not better than random."

^fThe summary excludes surrogates that included biotic variables and excludes tests that evaluated how well surrogates represented functional groups.

Table 2. Results of tests of the ability of abiotic surrogates to represent species, summarized by broad taxonomic group.

Taxon	Test result			Studies ^a
	positive	null	negative	
Vertebrates and plants combined	6	5	0	Grantham et al. 2010; Araujo et al. 2001
Bats	7	9	5	Ferrier & Watson 1997
Birds	18	20	2	Ferrier & Watson 1997; Grantham et al. 2010; Bonn & Gaston 2005; Beier & Albuquerque 2015; Araujo et al. 2001
Fish	81	64	70	van Wylsberge et al. 2012; Dalleau et al. 2010 ^b ; Janochowski-Hartley et al. 2011
Reptiles and amphibians ^c	16	29	3	Ferrier & Watson 1997; Grantham et al. 2010; Araujo et al. 2001; Hortal et al. 2009; Beier & Albuquerque 2015
Invertebrates: ants	0	20	1	Ferrier & Watson 1997
Invertebrates: beetles	6	13	2	Ferrier & Watson 1997
Invertebrates: spiders	1	20	0	Ferrier & Watson 1997
Mammals	6	5	2	Grantham et al. 2010; Araujo et al. 2001; Beier & Albuquerque 2015
Plants (fossil pollen)	0	2	0	Williams et al. 2012
Plants (terrestrial)	91	72	3	Ferrier & Watson 1997; Trakhtenbrot & Kadmon 2006; Grantham et al. 2010; Sarkar et al. 2005; Araujo et al. 2001; Beier & Albuquerque 2015
Plants: vegetation types	3	0	0	Bonn & Gaston 2005; Schloss et al. 2011

^aListed in order of number of surrogacy tests (largest to smallest).

^bOnly study to test abiotic surrogates for marine algae, marine invertebrates, and corals. In each case, all surrogacy test results (9–10 per taxon) were positive.

^cThese pooled results include results for amphibians (1–1–0, Araujo et al. [2001] and Beier & Albuquerque [2015]), reptiles and amphibians combined (2–0–2, Hortal et al. [2009]), frogs (1–7–2, Grantham et al. [2010]), and reptiles (2–21–9, Ferrier & Watson [1997], Grantham et al. [2010], and Beier & Albuquerque [2015]).

The proportion of positive surrogacy tests exceeded 50% only for plants (91 positive, 72 null, and 3 negative), vegetation types (3, 0, and 0, respectively), and studies that combined results for vertebrates and plants (6, 5, and 0) (Table 2). Neither SAI nor the proportion of positive surrogacy tests varied with the size of study area.

Of 330 tests for which SAI could be calculated, the median SAI was 0.08 (interquartile range –0.08 to +0.24; 36% of SAI scores < 0), and only 9 SAI values exceeded 0.60. For 80 SAI tests involving plants, the median SAI was 0.21 (interquartile range 0.14–0.27, with only 2 SAI < 0 [2.5%]). One surrogate strategy, the environmental diversity (ED) surrogate implemented by Beier and Albuquerque (2015) (8 tests) had median SAI 0.42 and interquartile range 0.27–0.68; these tests included 3 of the 9 instances of SAI > 0.60.

Effect of Choice of Abiotic Variables and Their Weighting

Abiotic diversity was characterized by 3–39 variables per surrogacy test. Each variable conveyed one of the 6 types of information, namely, climate (12 of 14 studies), topography (12 studies), energy (7 studies), soil and substrate conditions (10 studies), plant productivity (5 studies), or geographic space (one study that used latitude and longitude). Most studies used variables conveying 3 or 4 types of abiotic information (Table 1). Only 1 of 15

terrestrial studies (Ferrier & Watson 1997) considered hydrological variables (topographic wetness).

Ferrier and Watson (1997) was the only study that examined how increasing the number of variables affected surrogacy tests. They tested 3 groups of abiotic variables, one with 4 variables, one with 18 variables, and one with 22 variables. Contrary to their expectations, the surrogates defined by 4 variables performed better (23 positive, 17 null, and 0 negative test results) than the surrogacy tests with 18 variables (12–45–3) or 22 variables (3–39–6). Ferrier and Watson (1997) concluded that the first 4 variables (mean annual precipitation, mean rainfall, soil fertility, and ruggedness) were the main drivers of species turnover such that adding additional variables produced surrogates that were less related to species turnover than the surrogates using only the important variables.

Three studies compared performance of biotically informed surrogates to surrogates using unweighted variables. To create informed surrogates, species inventories from a subset of sites were used to optimally select the variables with greatest influence on species turnover, or weight each variable in proportion to its influence on species turnover. Sutcliffe et al. (2015) compared 2 sets of 35 multivariate clusters, one set based on standardized raw abiotic variables and another set in which each variable was nonlinearly transformed to reflect its influence

on species turnover (as determined from a previous study). The mean proportion of 482 marine species not meeting the target was 20–27% lower when sites were selected using biotically weighted abiotic clusters compared to sites selected using unweighted clusters. Ferrier and Watson (1997) found that biotically informed surrogates represented reptiles and forest trees better (SAI 0.19 for reptiles and 0.30 for trees) than surrogates using unweighted abiotic variables (0.03 and 0.12, respectively). Although Januchowski-Hartley et al. (2011) did not find that biotically informed surrogates represented fish species better, they suggested that surrogate performance would have improved if one additional biotically important variable (location above or below the main escarpment in the planning region) had been included.

Effect of Statistical Procedure Used to Define Abiotic Space

Four methods were used to define abiotic surrogates. The simplest method partitioned each abiotic variable into several equal-interval bins and treated each univariate bin as a surrogate. Thus, 3 variables, each divided into 10 bins, would yield 30 surrogates to be represented in a reserve system. The second method, which we labeled the overlay method, began with partitioning of each abiotic variable into classes, where the cut points were selected to produce equal intervals or equal numbers of cases per class, or to reflect ecologically meaningful thresholds. Then a cross-classification defined multivariate bins, such as “1000–2000 m elevation, 20–40% slope,” which were used as surrogates. Unlike the first method, these surrogates reflected all combinations of variable values; 3 variables each divided into 10 bins would yield 1000 surrogates (i.e., 10^3). In the third method, multivariate clustering was used to identify “lumps” in multivariate space; these were then used as surrogates. In the fourth approach, the environmental diversity (ED) approach, abiotic diversity was characterized without creating bins (Faith & Walker 1996a). Instead, ED uses a p median or minisum criterion to select individual sites that maximize coverage of environmental space (Faith & Walker 1996a, 1996b). Because the ED approach fully samples environmental space, it seems more likely to sample distributions of all species.

Ferrier and Watson (1997) was the only study that compared 2 or more of the 4 ways of defining abiotic surrogates. Surrogates defined by overlay procedures performed better (23–17–0) than surrogates defined by multivariate clusters (14–75–12) or p median (14–53–1). The authors believed that overlay performed better because the class boundaries were chosen to reflect species distribution patterns, whereas the clustering and p median analyses were biotically uninformed. Because of differences in study area, target species, thematic resolution, the way effectiveness was calculated, and size of selection units, we could not compare procedures across studies.

For instance, it would be inappropriate to conclude that choice of statistical procedure (overlay vs. ED) was the sole reason why abiotic surrogates performed poorly for Williams et al. (2012) and well for Beier and Albuquerque (2015).

Effect of Thematic Resolution

Several studies of binning methods compared the impact of increasing thematic resolution (i.e., the number of bins) on surrogacy tests, controlling for study system. Ferrier and Watson (1997), Sarkar et al. (2005), Januchowski-Hartley et al. (2011), and Dalleau et al. (2010) each reported that increasing thematic resolution improved surrogacy outcomes (Table 3). Hermoso et al. (2013) reached the same conclusion using synthetic data and demonstrated that the result was not due to larger areas being selected as thematic resolution increased. Within the multivariate clustering approach, Trakhtenbrot and Kadmon (2006) found that surrogate effectiveness varied among 6 clustering algorithms and among 6 ways of weighting variables.

Effect of Size of Selection Units

The smallest selection units (sites) were ~ 0.1 ha (the size of the marine survey plots used by Dalleau et al. [2010] and van Wynsberge et al. [2012]) and 4 ha (a bit larger than the terrestrial survey plots used by Ferrier and Watson [1997]). Williams et al. (2012) used the largest sites, namely, polygons averaging 24,000 km² (range $\sim 10^3$ to 10^6 km²). Four studies systematically varied size of sites to estimate the impact on SAI (Table 1). In 2 marine studies (Dalleau et al. 2010; van Wynsberge et al. 2012), SAI was higher for ~ 15 -ha sites than for smaller or larger sites, apparently because the smallest sites failed to reflect the influence of nearby conditions and because the mean abiotic conditions in larger sizes did not characterize conditions in the small survey plot at the center of the site. Ferrier and Watson (1997) found that SAI_{\log} did not vary between 2 sizes (4 ha, 2500 ha). Sarkar et al. (2005) found no influence of site size (7 sizes ranging from ~ 1 to ~ 100 km²) on SAI.

Discussion

Additional studies are needed to answer our primary question of whether abiotic surrogates can efficiently represent biodiversity. Across all taxa, abiotic surrogates improved on random selection of sites by only about 8% (median SAI 0.08) and in only 44% of 622 tests. Abiotic surrogates represented plants and vegetation types relatively well (56% of tests positive; median SAI 0.20), probably because plants are more closely tied to abiotic conditions than more mobile organisms. We believe this

Table 3. Number of bins or clusters used to define abiotic surrogates in each study, and results of increasing the number of bins or clusters for those tests that varied the number of bins or clusters while holding other conditions constant.

<i>Citation</i>	<i>Statistical method</i>	<i>Number of bins of clusters</i>	<i>Results of surrogacy tests (positive-null-negative) for studies that varied the number of bins or clusters^a</i>
Bonn & Gaston 2005	clustering	117	—
Dalleau et al. 2010	overlay	6 bins	23-0-0; mean SAI ₉₅ = 0.024
		15 bins	25-0-0; mean SAI ₉₅ = 0.078
Ferrier & Watson 1997	overlay and clustering	20 clusters	20 clusters: 2-15-3 (10%)
		50 clusters	50 clusters: 8-46-6 (13%)
		81 overlay bins	81 overlay bins: 23-17-0 (58%)
		125 clusters	125 clusters: 4-14-3 (19%)
Grantham et al. 2010	overlay	40 overlay bins	—
Januchowski-Hartley et al. 2011	3 clustering procedures	2, 4, 6, or 8	all results null, but SAI increased with number of bins for most surrogates
Sarkar et al. 2005	univariate bins	Quebec: 32, 42, 51, 56	mean SAI = 0.50 for 51 or 56 bins; mean SAI = - 0.79 for 32 or 42 bins
		Queensland: 30, 40, 49, 54	no trend (but all SAI were 0.75 to 0.80)
Schloss et al. 2011	overlay	41	—
Sutcliffe et al. 2015	clustering	35	—
Trakhtenbrot & Kadmon 2005, 2006	clustering	28	—
van Wynsberge et al. 2012	overlay	varied	impossible to unbundle number of bins from the type of abiotic variables
Williams et al. 2012	overlay	number of bins not stated	—

^aAbbreviation: SAI, species accumulation index.

level of support justifies the cautious use of abiotic surrogates to represent plants and plant communities.

We agree with Ferrier (2002) that null results (about the same as random) are not necessarily bad. To the extent that protected areas have been established in locations unsuitable for economic development and productive environments are underrepresented in our reserve systems (Sanderson & Watson 2015 [this issue]), random selection may be better than some current practices for selecting protected areas.

Two types of surrogate seem particularly promising. The ED approach as implemented by Beier and Albuquerque (2015) was 42% as effective as having knowledge of species locations (median SAI 0.42), and 7 of 8 SAI values were significantly positive. Originally proposed by Faith and Walker (1996a, 1996b), ED avoids 2 drawbacks of the alternative methods, all of which use categorical bins and are, therefore, unable to select sites on the basis of environmental differences among bins and environmental differences among sites within bins. We believe ED performed well because it selects sites to optimally span environmental space without the arbitrary constraints of binning methods. The biotically informed environmental clusters (i.e., clusters in which variables were weighted according to their influence on species turnover across space, as determined in an independent study) used by Sutcliffe et al. (2015) represented species about 25% better than clusters defined using raw

variables. The paired nature of this study (biotically informed vs. raw variables, holding other factors constant) strongly supports the inference that using biotic information improved surrogate performance. The fact that biotically weighted environmental variables explained 84% of the variation in species turnover among sites, compared with 41% for unweighted variables (Faith & Ferrier 2002), further supports biotic weighting. Multivariate procedures such as gradient forests (Ellis et al. 2012) can identify the variables that most affect species turnover. Weighting variables in terms of their influence on species turnover requires inventories of some sites in the planning area, which could increase the cost of biotically informed approaches.

Null or negative tests of abiotic surrogates should always be viewed as provisional because it might be possible to modify the surrogacy approach to produce more effective surrogates for the same study area and taxonomic group. For example, ED had appeared to perform poorly in two tests on vertebrates in Western Europe (Araujo et al. 2001; Hortal et al. 2009). But when Beier and Albuquerque (2015) made the improvements recommended by Faith (2011), ED achieved dramatically better results for the same Western European study area and vertebrate groups. In this regard, evaluation of abiotic surrogates differs from evaluation of cross-taxon surrogates. For cross-taxon surrogates (e.g., using birds as a surrogate for all species), the procedures and variables

used to define bird species are not scrutinized and are not part of the evaluation of birds as a surrogate. Evaluation simply consists of selecting sites to represent birds and evaluating incidental representation of other species. In contrast, evaluations of abiotic surrogates are, in fact, evaluations of the procedures applied to a particular set of environmental variables to define the individual surrogate classes that are then targeted for selection (Anderson et al. 2015).

This demonstrated improvability of abiotic surrogates justifies continued experimentation and evaluation. Based on our review, we suggest three practices that should improve abiotic surrogates.

First, we recommend considering several abiotic variables related to species turnover that were rarely or never considered in the studies we reviewed. For example, in coastal planning areas, the distance to the ocean may drive species turnover in cismontane sites (Ackerly et al. 2010), and likewise, the position of a stream reach above or below an escarpment may be a crucial variable governing fish assemblages (Januchowski-Hartley et al. 2011), but these variables were not used in any test. Similarly, geographic distance is an important driver of species turnover for less-vagile species (Soininen et al. 2007), but variables related to geographic separation were used in only 1 of 622 tests. Likewise, a few studies used readily available variables such as topographic wetness, presence of perennial or ephemeral waters, or variables quantifying within-site variability in topography, despite many studies documenting that these variables drive species turnover (Lawler et al. 2015). Using variables known to affect species turnover to define surrogates is likely to produce better surrogates.

Second, we recommend using fine thematic resolution to define abiotic surrogates because finer resolution improved results in all 5 studies that systematically varied resolution. For example, if a conservation planner has a fixed budget and costs of each unit are relatively uniform, the planner using a multivariate clustering procedure could set the number of bins equal to the largest number of units within budget, as Bonn and Gaston (2005) did. Alternatively, the planner could use the ED approach, which has unlimited thematic resolution.

Third, we recommend against using extremely large units of selection. In two studies that evaluated the influence of site size, SAI was higher for sites of about 15 ha than for larger or smaller sites. A key assumption of using surrogates is that the values of abiotic variables in a site reflect conditions experienced by the site's species. In a large site, the mean slope or mean insolation (for example) may occur nowhere in the cell such that no species experiences the mean values. This problem can be minimized by using small to midsized sites and by using measures of within-site variability rather than the mean (Araujo et al. 2001) or the centroid value (Williams et al. 2012). A site can be too small if it excludes

important environmental interfaces, e.g., between soil types or topographic features (van Wynsberge et al. 2012) or if site size is finer than the resolution at which abiotic conditions are mapped. We believe the critical factor is not so much the size of the selection unit, but how well a polygon of a particular size captures the physical environment relevant to the species of interest.

Using and Evaluating Abiotic Surrogates in Conservation Planning

The 14 studies we evaluated provided moderate support for the effectiveness of abiotic surrogates in representing plants but weak or mixed support for effectiveness representing other taxonomic groups. The two most promising types of surrogates (ED and biotically informed clusters) need additional evaluations to fully assess their utility. We are optimistic that additional improvements and rigorous testing will soon provide broadly reliable abiotic surrogates, or, at a minimum, useful guidance on the analytic steps (choice of variables, statistical procedures, and site sizes) and ecological conditions (climate zones, biotic realms, and degree of human influence) under which abiotic surrogates are reliable.

Until such rigorous testing has occurred, how can a conservation planner responsibly use abiotic surrogates? One option is that species inventories in a subset of planning units could be used to make inferences about which variables influence species turnover (and hence should be used to define surrogate) or to test effectiveness of the surrogate using SAI. To avoid a circular test of surrogacy, the data used to select or weight variables should be independent of the data used to evaluate the surrogate. We suggest that perhaps 50 inventory sites might be needed to select or weight variables (Osborne & Costello 2004) and perhaps 30 plots might be needed for evaluation. (van Wynsberge et al. [2012] found that SAI was extremely sensitive to reduction below 27 evaluation sites.) Although the cost of these inventories would not be trivial, it could be a reasonable investment if planners are using surrogates to prioritize thousands of sites.

A planner could also use an untested surrogate when the planner is prioritizing sites to represent well-justified targets (e.g., vegetation types and mapped occurrence of rare species or assemblages) and wishes to simultaneously increase abiotic heterogeneity. The case studies presented by Anderson et al. (2015) show that achieving targets for abiotic diversity usually does not increase in the total area prioritized and does not decrease the achievement of other targets. Under these circumstances, using abiotic surrogates is a low-cost type of bet hedging.

In the context of using geophysical surrogates as a climate adaptation strategy, more evaluations of surrogates based on nonclimate abiotic variables are needed. Such surrogates would indirectly favor selection of climate-diverse reserves because some nonclimate variables (e.g.,

elevation, distance to coast, and insolation) are important drivers of local climate (Ackerly et al. 2010; Dobrowski 2011). In addition to improving species representation, abiotic surrogates can help conservation planners identify areas that will support the processes that generate and maintain biodiversity such as edaphic interfaces, sand movement corridors, and interbasin riverine corridors (Cowling et al. 2003).

The need for inexpensive abiotic surrogates in data-poor regions, and as a climate adaptation tool in all regions of the globe, should motivate efforts to improve the effectiveness of abiotic surrogates in coarse-filter conservation planning. We hope our review promotes such efforts. Finally, we advocate that abiotic surrogates should complement, and not replace, strategies that aim to represent the current diversity of species and natural land cover types.

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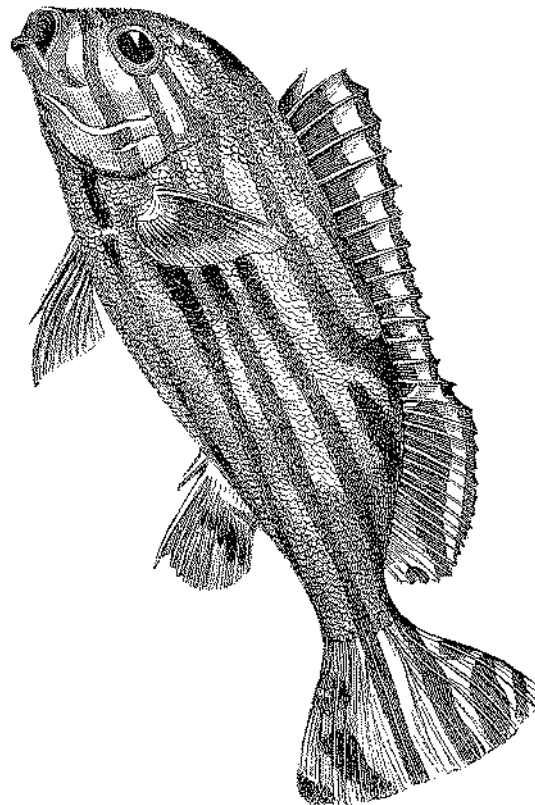
Supporting Information

Supplemental methods and discussion (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.

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Beier et al. Improving the use and evaluation of abiotic surrogates in conservation planning: a review of selection-based surrogacy tests

Introduction

We considered conducting a formal meta-analysis of studies, but were discouraged from doing so by the small number of independent studies (13) and the fact that we could calculate variance in SAI for only 3 studies. In a meta-analysis the effect size for each study is weighted by the inverse of its variance (Borenstein et al. 2009). Variance in SAI can be estimated in one of 2 ways. First, the investigator could apply the treatment (selection of sites using the surrogate) to multiple landscapes, just as a study of effectiveness of a medicine would give the medicine to multiple patients. Three studies did take this approach (Grantham et al. 2010, Hortal et al. 2009, Sarkar et al. 2005), but each had only 2 landscapes, and in two cases the landscapes were not independent (one of Hortal et al.'s landscapes was a subset of the other and Grantham et al.'s 2 landscapes were adjacent to each other), precluding an unbiased estimate of variance. Second, if the surrogate was applied using a stochastic algorithm such as Marxan or Zonation, the investigator could repeatedly apply the surrogate to the same landscape, estimate effectiveness of each trail, and calculate variance across trails. None of the studies we reviewed took this approach.

It is tempting but wrong to think that the 95% confidence band for the random curve (reported by several studies) provides a way to estimate variance of the surrogate. The variance among performance of sets of randomly selected sites is not the variance in the performance of sets of sites selected using the surrogate. By analogy, one could give a medicine to *one* patient and compare that patient's response to mean and variance of a large control (random) group; this reveals

something about the probability the observed level of improvement in the one observed patient could have occurred by chance without the medicine, but it reveals nothing about the variability in patient response to the medicine. If the SAI is well above (or below) the 95% CI for the random curve, this finding would increase confidence that the surrogate performed well *for that landscape*, but it does not justify giving greater weight to that particular study in a meta-analysis. To do so would be tantamount to assuming that the CI of the random outcomes explains how the surrogate (or medicine) would perform for other landscapes (or patients). The random CI does **not** reflect the precision with which the effect size [surrogate effectiveness] has been estimated (Borenstein et al. 2009: p. 5). Instead it reflects the precision with which effectiveness of a random selection procedure has been estimated.

Tallying the proportion of studies that reported significant p-values is sometimes treated as a type of meta-analysis. However such "vote-counting" conflates statistical and biological significance in a way that can lead to misleading conclusions, and has a strong systematic bias toward "no effect" conclusions (Borenstein et al. 2009).

The objectives listed in the main paper included investigating how surrogate performance was affected by choice of abiotic variables, statistical procedures, thematic resolution of variables, and size of sites. In addition we considered how surrogate performance was affected by the type of biotic information used to evaluate surrogates. We expected the most optimistic results from evaluations using species distribution models because these models are prone to false presences, intermediate results for species

inventories, and the most pessimistic results from evaluations using occurrence records (e.g., museum records) because these data are prone to false absences.

Methods

In most surrogacy tests reporting SAI, incidental representation was the percentage of targets achieved, where achievement was a binary response (species represented or not). For studies in which the target was to represent a certain percentage of each species' distribution or abundance in the surrogate-based reserve, target achievement was expressed as the mean percentage of range or abundance captured in the sites. We rescaled these results to the interval 0 to 1 using $(S - R)/(O - R)$ and interpreted the rescaled results as SAI values.

We modified the SAI thresholds for papers reporting two variants of SAI, namely SAI_{log} and SAI_{95} . Our modifications followed the same rationale as Rodrigues and Brooks (2007) except that we used empirical data (not available to Rodrigues and Brooks) to modify the thresholds.

Calculating the difference between SAI and SAI_{log}

SAI_{log} , calculated as $[\log(S) - \log(R)]/[\log(O) - \log(R)]$, (S, R, and O defined in Fig. 1) is always more extreme (further from 0) than SAI. We calculated this difference for every test that provided values for S, R, and O. These data consisted of 4 tests in Hortal et al. (2009), 8 tests in Sarkar et al. (2005), 1 test in Schloss et al. (2011), and 62 tests in Trakhtenbrot and Kadmon (2005, 2006). Across these 75 tests, the median difference was 0.04 and the mean difference was 0.13. Accordingly, we considered a surrogacy test to have a positive result when $SAI_{log} > 0.15$, a negative result when $SAI < -0.15$, and otherwise a null result.

Calculating the difference between SAI and SAI_{95}

The other variant, SAI_{95} is calculated as $(S - R_{95})/(O - R_{95})$, where R_{95} is the upper value of the 95% confidence interval of the random curve or point (Fig 1.) Hortal et al. (2009) presented 4 SAI_{95} values and presented the raw values of S, R, and O needed to calculate SAI for the same surrogacy tests. Van Wylsberge et al. (2012) reported the difference between the upper 95% confidence limit and the mean of 1000 random sets of sites for each of 6 scenarios. These data allowed us to calculate 10 mean differences between SAI and SAI_{95} . Across these 10 tests, the mean and median difference was 0.64 (range 0.53 to 0.78). Accordingly, for the 58 tests for which only SAI_{95} could be calculated, we considered a surrogacy test to have a positive result when $SAI_{95} > -0.20$, a negative result when $SAI_{95} < -0.40$, and otherwise a null result.

How surrogate performance was affected by the type of biotic information used to evaluate surrogates

Most (7 of 13) studies used species inventories of particular taxa (Table 1) to evaluate incidental representation of sites selected to represent surrogates. Biotic inventories were typically collected on 1 (rarely 2) plot per site, and survey plots were typically < 1 ha.

Five studies (Araujo et al. 2001, Hortal et al. 2009, Sarkar et al. 2005, Trakhtenbrot & Kadmon 2005, 2006, Williams et al. 2012) used species occurrences collated from museum records, checklists, and other non-inventory data. Occurrence data are prone to false absences (Elith et al. 2006). Three studies used species distribution models for some species (Grantham et al. 2010, who used inventories for other species) or all species (Januchowski-Hartley et al. 2011, Sutcliffe et al. in review) in the focal taxon. These models

may be prone to false presences (Rodrigues & Brooks 2007). In the only direct comparison of 2 types of biotic data (Sutcliffe et al. in review), SDMs did not produce markedly more optimistic evaluations of surrogates than produced by inventory data.

In a study with only 27 inventory plots, Van Wynsberge et al. (2012) found that the outcome of 90% of surrogacy tests changed significantly (including changes among null, positive, and negative inferences) with the removal of a single survey plot.

Discussion

How surrogate performance was affected by type of species data used to evaluate surrogates

Rodrigues and Brooks (2007) argued that evaluation of incidental representation should use species inventories instead of species distribution models (SDMs) or occurrence records. They argued tests using SDMs are overly optimistic because modeled distributions are prone to errors of commission (false presences – Hurlbert & Jetz 2007). However false presences increase all 3 terms in SAI (calculated as $(S-R)/(O-R)$), so the overall impact is not obvious. In the only side-by-side comparison of evaluations using SDMs versus inventories (Sutcliffe et al. in

review), SDMs did not produce markedly more optimistic evaluations. Another issue is that SDMs are driven by some of the same variables used to define abiotic diversity, making the test somewhat circular. If SDMs are used, the SDMs should be built from data collected in the planning area.

Species occurrence records may produce overly pessimistic estimates of incidental representation because of false absences, which can vary among cells for reasons unrelated to abiotic conditions, such as distance from a research station (Elith et al. 2006).

Species inventories avoid the potential circularity of SDMs, and are less prone to errors of omission than occurrence records. Errors of omission can be minimized by rigorous inventory effort and ensuring that the inventory plot is representative of the entire site.

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Case studies of conservation plans that incorporate geodiversity

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Abstract: *Geodiversity has been used as a surrogate for biodiversity when species locations are unknown, and this utility can be extended to situations where species locations are in flux. Recently, scientists have designed conservation networks that aim to explicitly represent the range of geophysical environments, identifying a network of physical stages that could sustain biodiversity while allowing for change in species composition in response to climate change. Because there is no standard approach to designing such networks, we compiled 8 case studies illustrating a variety of ways scientists have approached the challenge. These studies show how geodiversity has been partitioned and used to develop site portfolios and connectivity designs; how geodiversity-based portfolios compare with those derived from species and communities; and how the selection and combination of variables influences the results. Collectively, they suggest 4 key steps when using geodiversity to augment traditional biodiversity-based conservation planning: create land units from species-relevant variables combined in an ecologically meaningful way; represent land units in a logical spatial configuration and integrate with species locations when possible; apply selection criteria to individual sites to ensure they are appropriate for conservation; and develop connectivity among sites to maintain movements and processes. With these considerations, conservationists can design more effective site portfolios to ensure the lasting conservation of biodiversity under a changing climate.*

Keywords: abiotic surrogates, conservation planning, conserving nature's stage, geodiversity

Estudios de Caso de Planes de Conservación que Incorporan a la Geodiversidad

Resumen: *La geodiversidad se ha usado como un sustituto de la biodiversidad cuando la ubicación de las especies es desconocida y esta utilidad puede extenderse a situaciones en las que la ubicación de las especies está en cambio constante. Recientemente, los científicos han diseñado redes de conservación que buscan representar explícitamente la gama de ambientes geofísicos, al identificar una red de estados físicos que podrían mantener a la biodiversidad mientras permiten cambios en la composición de las especies en respuesta al cambio climático. Ya que no existe una estrategia estándar para diseñar dichas redes, compilamos ocho estudios de caso que ilustran la variedad de formas con las cuales los científicos han enfrentado el reto. Estos estudios muestran cómo se ha dividido la geodiversidad y cómo se ha usado para desarrollar portafolios de sitios y diseños de conectividad; cómo los portafolios basados en geodiversidad se comparan con aquéllos derivados de las especies y las comunidades; y cómo la selección y la combinación de variables influye sobre los resultados. Colectivamente, los estudios sugieren cuatro pasos clave al usar la geodiversidad para*

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aumentar la conservación basada tradicionalmente en la biodiversidad: crear unidades de suelo a partir de las variables relevantes para las especies combinadas de una forma significativa ecológicamente; representar las unidades de suelo en una configuración espacial lógica e integrarlas con la ubicación de las especies de ser posible; aplicar criterios de selección a los sitios individuales para asegurar que son adecuados para la conservación; y desarrollar la conectividad entre sitios para mantener los movimientos y los procesos. Con estas consideraciones, los conservacionistas pueden diseñar portafolios de sitio más efectivos para asegurar la conservación duradera de la biodiversidad bajo un clima cambiante.

Palabras Clave: conservación del estado de la naturaleza, geodiversidad, planeación de la conservación, sustituta abiótica

Introduction

Geodiversity has been incorporated into conservation plans as a coarse filter for capturing diverse species and communities, as a biodiversity surrogate when biotic information is not available (Hunter et al. 1988; Faith & Walker 1996), and as a direct target for representation (Spicer 1987). Recently, geodiversity has garnered renewed attention as conservationists recognize the transient nature of biotic patterns and search for a more enduring framework around which to organize land protection under a changing climate. Defined as the natural range of geological, geomorphological, and soil features (Gray 2013), *geodiversity* characterizes the available physical environments and shapes species distribution patterns both directly and through its influence on climate (Anderson & Ferree 2010). Using geodiversity, scientists can design conservation networks that represent the range of physical environments of a region, thus capturing the heterogeneity necessary to sustain a diversity of species and ecological processes, while allowing for change in species composition in response to climate change (Beier & Brost 2010). Here, we present 8 case studies that integrated geodiversity into conservation plans designed to support both current and future biodiversity.

To incorporate geodiversity into quantitative planning, it is often necessary to partition it into ecologically meaningful spatial units, map the distribution of those units, and assess their representation, abundance, and configuration. The availability of high-resolution (10–90 m) digital elevation models (DEMs), digitized maps of soils and geology, and interpolated surfaces of insolation or solar radiation, have made it practical to perform such assessments across large geographic regions. However, there are many ways to quantify the geophysical elements that influence species distributions and no single best approach has yet emerged to identify a meaningful geophysical template for conservation. The case studies presented here can help conservation biologists begin to understand the implications of variable choices, combination methods, and the effects of scale (Table 1).

The authors of this paper are all conservation scientists actively involved with testing and applying geodiversity to conservation planning, and each case study illustrates an important method, issue, or conclusion. Most of these studies focus on the delineation and representation of geophysical units, but some also address spatial processes such as the arrangement of topographically based microclimates or the degree of connectedness across units. The 8 studies are a mix of published and unpublished research (Supporting Information), and 6 of them summarize applied projects that were used to inform conservation decisions.

The case studies focus on terrestrial ecosystems and illustrate the key issues related to how geodiversity is measured and integrated into site prioritization. The first 2 studies describe 2 common and virtually synonymous methods used in the United States for mapping recurring geophysical land units: ecological land units (case study 1) and land facets (case study 2), and illustrate how they have been used to design conservation portfolios and identify corridors respectively. The next 3 studies (case studies 3–5) compare prioritization based on geodiversity to prioritization based on biodiversity, using conservation portfolios developed by The Nature Conservancy (TNC). Case studies 6 and 7 examine the sensitivity of site prioritizations to the choice of geophysical variables, the spatial resolution of the data, and the method used to define land units as multivariate entities. Finally, case study 8 illustrates a gradient approach to partitioning abiotic space to elucidate trade-offs in conservation planning.

Terminology for describing and labeling geodiversity spatial units has not been standardized. Here we use the following conventions: *abiotic diversity* to refer to geodiversity and climatic diversity; *geodiversity* to describe geologic, geomorphologic, and soil features; *geophysical setting* to describe large regions (thousands to millions of hectares) dominated by a single geology class; *land unit* to describe the synonyms *ecological land unit* (Anderson 1999) or *land facet* (Beier & Brost 2010), which are particular combinations of geodiversity features that characterize local landforms (e.g., high elevation, steep ridge).

Table 1. Comparison of attributes, data, and methods across 8 case studies of conservation plans that incorporate geodiversity.

	Case study							
	1	2	4	5	6	3	7	8
Region	western US	south-western US	north-western US	north-western US	north-western US	north-eastern US	south-western US	New South Wales AU
Analysis method	Marxan ^a	least-cost modeling	Marxan ^a	Marxan ^a	Marxan ^a	statistical scoring	statistical scoring	DIVERSITY ^b
Site prioritization criteria	optimization of 100s of land units	optimization of 5–15 land units	optimization of 41 land units	optimization of 121 land units	optimization of 7–3,884 land units	Z scores of hexagons relative to 29 settings	relative land-unit diversity value by ecoregion	maximum complementarity in environmental space
Selection of variables and thresholds	expert opinion and vegetation patterns	statistical clusters	expert opinion	correlation of variable with vegetation maps	expert opinion and sensitivity tests	rare species overlay and regression of species diversity on geodiversity overlay	statistical thresholds using minimum variance or equal subsets overlay (cluster also tested)	expert opinion
Method for combining variables	overlay	cluster	cluster	overlay	overlay, cluster, and hybrid			
Grid cell size (m)	30 and 90-	30	240	270	270 and 1 km	30	90 and 270	1.0
Planning unit size	1,200–1,500 ha hexagons	30-m cell or aggregates	HUC ^c 12	270-m cell	HUC ^c 12	404 km hexagon	1–23 km ² moving windows	0.1 × 0.1 degree grid cell
Elevation source ^d	30 and 90-m DEM	30-m DEM	30-m DEM	270-m DEM	30-m DEM	30-m DEM	90-m DEM	1-m DEM
Elevation partitioning	3–10 zones	continuous	continuous	6–10 zones	variable	3 zones	minimum variance and equal subsets	continuous

Continued

Table 1. Continued.

	Case study							
	1	2	4	5	6	3	7	8
Topography source ^d	30 and 90 DEM	30-m DEM	30-m DEM	270-m DEM	30-m DEM	30-m DEM	90-m DEM	1 m DEM
position	Y	Y			Y	Y		
slope	Y	Y	Y	Y	Y	Y	Y (THL) ^e	
aspect	Y	Y				Y	Y (CTI) ^f	
Wetness	Y					Y		
Geology Source	state maps ^g				state maps ^g			
Surface	6–10 classes				9 classes			
Geology								
Soil source	state surficial maps ^h			STATSGO ⁱ 1:250,000	STATSGO ⁱ 1:250,000	Soller 1998 ^j , SURGO ^b 1:24,000	SURGO ^b 1:24,000	
texture			Y	Y	Y	Y	Y (suborder)	
order								
depth			Y		Y			
Available water capacity			Y		Y			
Org spell out					Y			
Content								
Bulk Density								
Climate source			CIG ^j 1/16th degree		Y			ESOCIM ^k
temp and precipi- tation			Y					Y

^aBall and Possingham (2000).^bSoftware package for sampling phylogenetic and environmental diversity (Walker & Faith 1994).^cThe USGS hydrologic cataloging unit. A cataloging unit is a geographic area representing part of all of a surface drainage basin, a combination of drainage basins, or a distinct hydrologic feature.^dGesch et al. (2002), Oregon Geospatial Data Clearinghouse (1999), the Washington Department of Natural Resources (2002), and the Idaho Geospatial Data Clearinghouse (2004).^eTopographic beat load (McCune & Keon 2002).^fCompound topographic index (Moore et al. 1993).^gBedrock and surficial geology maps compiled from individual state sources (various resolutions 1:100,000–1:1,000,000).^hSoil Survey Geographic (SSURGO) Database (NRCS 1995). SSURGO is incompletely mapped and most users supplemented this with STATSGO where needed (Soller 1998).ⁱState Soil Geographic (STATSGO) Database (NRCS 1994).^jSoller (1998). Quaternary sediments in the glaciated United States east of the Rocky Mountains (USGS Digital Data Series DDS-38).^kClimate Impacts Group (2011), ESOCIM (Hutchinson 1984).

Case Study 1: Incorporating Geodiversity into TNC Conservation Portfolios in the U.S. Intermountain West

In the 1990s, TNC developed ecoregional “portfolios” across much of the Americas, including all ecoregions of the United States. Each was intended to identify sites and strategies for conserving native biodiversity (Groves 2003), and each effort applied principles of systematic conservation planning (Margules & Pressey 2000) to identify a portfolio of conservation sites. In the western United States, the Marxan site selection software (Ball & Possingham 2000) was used to identify a portfolio of sites that met representation goals for each mapped vegetation type (Comer & Schulz 2007), and each of 100–300 vulnerable species. However, planners were concerned that the vegetation types (typically 30–40 per ecoregion) might not sufficiently represent within-type diversity, and that coarse filter portfolios (*sensu* Noss 1987) might be more robust to climate change if finer-grain environmental diversity was incorporated.

To address these concerns in four western ecoregions (Southern Rocky Mountains, Great Basin, Greater Yellowstone, Colorado Plateau [Supporting Information]), TNC modified each regional portfolio by adding targets for ecological land units (Anderson 1999). Each land unit was a combination of an elevation zone, a substrate class, and a landform type. Landforms were derived from a 30-m or 90-m DEM with slope, aspect, topographic wetness, and relative topographic position. Elevation zones were mapped using DEMs, and surficial geology maps were compiled from digitized state geology maps (Table 1). In each ecoregion, each variable was partitioned into discrete classes; breakpoints between classes were selected to reflect regional vegetation patterns or ecologically meaningful distinctions in elevation, soil chemistry, and drainage. Elevation zones followed long-established bioclimatic concepts, and surface geology classes emphasized soil chemistry and drainage. Landform classes reflected local vegetation responses to topographically driven temperature and moisture patterns. Commonly, 200–400 land units were mapped for each ecoregion with simple map overlay methods, and then these were further overlain with mapped vegetation types. For each vegetation type, knowledge of disturbance patch size and notions of minimum dynamic area (Pickett & Thompson 1978) were used to establish representation goals: a percentage of the current extent of each vegetation and land-unit combination and a minimum area threshold for each vegetation type.

The resulting portfolios are being used by TNC to guide conservation strategies. Land-unit methods ensured that the portfolios not only represented rare species and common vegetation types in sufficiently sized patches, but also fully captured the geodiversity within each

vegetation type. Thus, the results incorporated existing ecological gradients that will become increasingly important with climate change. Interestingly, no net increase in portfolio area was required to incorporate this combined measure of geophysical and biotic diversity than to capture biodiversity alone.

Case Study 2: Integrating Geodiversity Corridors with Focal Species Corridors to Prioritize Desert Lands in the U.S. Southwest

Penrod et al. (2012) developed linkage designs that would conserve connections between 22 pairs of large protected areas (PAs). The designs were requested by the U.S. Bureau of Land Management (BLM) facing proposals for industrial solar energy projects in the Mohave and Sonoran deserts of southeastern California. The BLM wanted broad, multi-stranded linkages to serve the needs of focal species (e.g., bighorn sheep [*Ovis canadensis*], desert tortoise [*Gopherus agassizii*]) under today’s climate and provide continuity and interspersed geodiversity to conserve metapopulations of all or most species as climate changes.

To map each linkage, Penrod et al. (2012) compiled 30-m DEMs and characterized each pixel with respect to three topographic position classes (ridge, slope, canyon) and 3 continuous variables (insolation, slope, and elevation [Table 1]). Rivers and ephemeral streams were mapped as riverine features. In each planning area, multivariate clustering was used to define 5–15 dominant land units (land facets *sensu* Beier & Brost [2010], such as “high elevation, steep ridge”) within the 2 PAs, and then each pixel in PAs and in the intervening matrix was assigned to 1 land-unit type. Each pixel was also given a diversity score based on the number and evenness of land units within a 200-m radius (Brost & Beier 2012a).

Within each PA, pixels of each land-unit type were aggregated into polygons (see Brost & Beier 2012b) and the larger polygons (over 2500 ha) served as termini for the corridor analysis between PAs. Least-cost modeling was used to identify 3 corridor types: a 2-km-wide corridor for each land-unit type (5–15 total), a corridor with high land-unit diversity, and a corridor for each of four focal species based on habitat suitability. To map the corridors connecting patches of similar land-unit types, individual pixel resistance scores were calculated as the multivariate dissimilarity from the characteristic values for that land-unit type. A corridor was discarded if it included a long segment of high resistance, such as when the termini for a rugged, high elevation land unit were separated by a large expanse of low desert flats. The 3 corridor types were combined with any riparian feature reaching both PAs, to form the linkage design. The final 22 linkage designs linked the 18 large PAs into a network that was

intended to support biodiversity under current and future climates.

In this approach, species corridors (fine filter) were intended to provide connectivity under current climate, and land-unit corridors (coarse filter) were intended to provide connectivity under future climate. Corridors with high facet diversity were intended to support interactions between species, and across land units, during periods of rapid change (Beier 2012).

Case Study 3: Identifying Climate-Resilient Sites for Conservation across Geophysical Settings in the U.S. Northeast and Maritime Canada

Anderson et al. (2014) developed a method to identify a portfolio of climate-resilient sites representing geodiversity in the northeastern United States and Canada and compared it with a portfolio selected for biodiversity. The results were used by TNC to identify new conservation areas and apply a climate-change lens to land acquisitions. Site resilience was defined as the expected ability of a site to support a diversity of native species and ecological functions in the face of climate change. Land units based on the ecological land unit models described in case study 1 were defined at 2 scales. At the coarser scale, the region was stratified into 29 broad geophysical settings based on 4 elevation zones corresponding to changes in dominant vegetation, and 9 substrate classes (7 bedrock and 2 surficial) defined by overlays of rare species locations and regression tests on total species diversity. The classes recognized unique bedrocks such as limestone and serpentine and common types such as granite (Anderson & Ferree 2010) and were intended to represent distinct species environments.

Within each geophysical setting, a finer scale measure of site resilience was assessed for each 30-m pixel based on landscape diversity and local connectedness. To measure landscape diversity, a landform model was created from a 30-m DEM using slope, topographic position, aspect, and wetness to identify 11 topographic landforms that reflected distinct temperature and moisture combinations (e.g., northwestern sideslope, wet flat). Local landscape diversity was measured as the variety of landforms, the elevation range, and the density of wetlands within a 40-ha circular search area. Local connectedness was measured using a resistant kernel model (Compton et al. 2007) on a 90-m, expert-derived, resistance grid created from land cover and roads (Homer et al. 2007; Tele Atlas 2012). Sites were scored based on a sum of diversity and connectedness normalized within each geophysical setting.

High-scoring sites (>0.5 SD above the mean for each geophysical setting) were compared with the sites prioritized in TNC's ecoregional portfolios based on rare

species and communities (Supplementary Information). The high-scoring sites captured 79% of the rare species taxa, 49% of their priority locations, and 53% of the priority locations for natural communities. When overlaid with a map of terrestrial vegetation types (Ferree & Anderson 2010), high-scoring sites captured all 98 of the vegetation types in amounts ranging from 1% to 91% of their respective area.

Anderson et al. (2014) concluded that this method offers a practical approach to conservation planning that captures a wide spectrum of rare and common targets while aiming to identify areas where species are most likely to persist given a changing climate. The method assumes that species persistence is more likely in connected areas with high micro-climate diversity (Weiss et al. 1988; Ackerly et al. 2010; Dobrowski 2011) and that the landscape between sites remains permeable.

Case Study 4: Comparing Conservation Priorities for Abiotic Units and for Biodiversity in the U.S. Columbia Plateau

Schloss et al. (2011) developed a potential reserve network selected to represent abiotic diversity and compared it with one selected to represent current biodiversity. From this, they identified regions where incorporating abiotic data could enhance a biodiversity-based network. To describe an abiotic reserve network, abiotic land units were created from nine topographic, edaphic, and climatic variables for the U.S. Columbia Plateau ecoregion. Elevation and slope were derived from 30-m DEMs. Data on three mapped soil properties were used as indicators of productivity: soil depth, available water storage, and particle size (Table 1). Maps of mean maximum temperature during the warmest month, mean minimum temperature during the coldest month, and mean total precipitation for both the wettest month and driest month were developed using 1/16th-degree resolution modeled climate surfaces averaged for 1915–2006 (Climate Impacts Group 2011). Data for all abiotic variables were aggregated to a 240-m grid.

The 9 variables were normalized and clustered into 41 abiotic land units across the Columbia Plateau using the *k*-means clustering algorithm. Conservation goals were to reserve 15% of the ecoregion, with an equal amount of PA in every unit. Reserve networks were created to efficiently represent the targeted area of every abiotic land unit using Marxan (Ball & Possingham 2000). The relative priority of each planning unit was calculated as the number of times (out of 1,000 Marxan runs) that each planning unit was included.

A separate Marxan parameterization was used to generate a biodiversity-based reserve network and to identify biodiversity-based conservation priorities based on

66 vegetation types and occurrences of 27 rare species mapped previously (Davis et al. 1999). Planning unit priority was compared between networks created to represent abiotic land units and networks created to represent biodiversity. Incidental representation of biodiversity targets was calculated as the percentage of biodiversity goals that were achieved in an abiotic-based network.

The 2 prioritizations resulted in different distributions of priority planning units. High priority planning units based on abiotic land units were mainly distributed at the margins of the Columbia Plateau ecoregion whereas high priority planning units based on biodiversity were largely in the interior. This may reflect Marxan's attention to complementarity, which prioritizes unusual combinations of land units, such as those at the transitional boundary of the region. Although few planning units were high priority for both abiotic facets and biodiversity, many planning units were of low priority in both networks. The abiotic-based network represented 76% of the vegetation types at target quantities but only 16% of the rare species.

Schloss et al. (2011) concluded that abiotic-based networks are effective at representing a large percentage of coarse-filter biodiversity targets, but the abiotic-based reserve network poorly represented current occurrences of rare species and did not provide a means for species to redistribute across the landscape. In regions where geodiversity-based priorities differ from biodiversity-based networks, high priority regions for abiotic units can be added to biodiversity-based conservation plans to make these networks more robust to the impacts of climate change.

Case Study 5: Ability of The Nature Conservancy's Biodiversity-Based Conservation Portfolio to Capture Geodiversity in the U.S. Northwest

Buttrick et al. (2014) assessed the ability of a portfolio of biodiversity-based conservation sites to capture diversity of land units derived from the intersection of soil, elevation, and slope in four ecoregions in the U.S. Pacific Northwest. The biodiversity sites were taken from TNC ecoregional portfolios developed between 1999 and 2007 (Columbia Plateau, Middle Rockies, East Cascades, Canadian Rockies [Supporting Information]) and aimed to capture rare species plus 10% to 30% of each mapped vegetation type within each ecoregion.

Before choosing variables to define land units, Buttrick et al. used measures of association to select ecologically meaningful variables and specify ecologically meaningful classes for continuous variables. For example, to select the most relevant soil-related variable, they cross-tabulated dominant mapped vegetation types (LANDFIRE 2009) with each potential soil variable (Table 1) and calculated an area-weighted measurement of association.

Because soil order was most closely related to dominant vegetation, it was selected as the substrate variable. A similar procedure was used to choose the elevation and slope classes but they found no significant relationship between class limits and vegetation. They then generated two sets of land units each with a resolution of 270 m². Both sets had 9 soil orders, but one had 6 elevation classes and 3 slope-aspect classes, and one had 10 elevation classes and 5 slope-aspect classes. Within each ecoregion, both sets of land units were overlaid with and compared to the TNC portfolio sites.

The overlay indicated that TNC's portfolios encompassed a wide range of geodiversity; across the four ecoregions, 91% of all land units had 30% or more of their area included in portfolios. This is likely because the portfolio was designed to capture dominant vegetation types and the geophysical variables were also selected and divided based on how well they reflected the pattern of vegetation distribution. Representation was not influenced by the number of slope or elevation classes. The percentage of an ecoregion in the portfolio (tested at 10, 20, and 30%) had little effect on how well geodiversity was captured.

Buttrick et al. concluded that planning to conserve geodiversity of an ecoregion is compatible with efforts to conserve biodiversity. Networks of conservation areas designed to conserve all of the biodiversity within an ecoregion also contain much of the geodiversity. Expanding them to encompass the full suite of geodiversity features seemed to be an inexpensive, prudent step to potentially enhancing the conservation of species and changing communities in the future.

Case Study 6: Sensitivity of Conservation Priorities to Decision Rules in Designating Land Units in the U.S. Pacific Northwest

J.L. and C.S. (unpublished, contact these authors for further information or data access) quantified how decisions about land-unit designation affected subsequent prioritization in three ecoregions in the U.S. Pacific Northwest. Land units were created in 3 ways: with topographic variables only, with topographic variables plus soil variables, and with topographic variables plus geologic type. Elevation and slope were used to identify areas of unique topography. Edaphic variables included soil order, organic matter, bulk soil density, soil depth, and available water capacity (Table 1). Geology compiled from state sources was classified into nine substrate classes as in case study 3. All data layers were converted to grids at both 270-m and 1-km resolution to explore the potential impact of resolution on land-unit definition.

Geophysical variables were combined into land units using one of three models: a simple overlay of variable classes, a statistical *k*-means clustering approach, which

identifies the most homogenous groupings of variables through an iterative process, and a hybrid of the 2. Conservation networks were generated using Marxan (Ball & Possingham 2000) to represent 30% of the area of each land unit from a given land-unit model. Highest priority was assigned to planning units that were included in all of the 1,000 Marxan runs. Correlation coefficients were used to measure the similarity in the priority of planning units based on different land-unit models.

Between 7 and 3,884 land units were produced and tested, depending on the combination of variables and modeling approach used. Resulting priorities were most different between land units developed with a clustering (*k*-mean and hybrid) approach and those developed with the overlay approach (correlation coefficients 0.33–0.68). Within any single approach (*k*-means, hybrid, overlay), priority rankings were highly correlated between land-unit sets developed with different variables or at different resolutions (between 0.72 and 0.93). Although there were differences in the prioritization of planning units, a network of the highest priority planning units selected to represent 30% of each land-unit type from a given set of land units also represented the land units created from other variables, resolutions, and approaches relatively well.

J.L. and C.S. concluded that the inclusion of soil or geology in addition to topography and the choice of data resolution made less of a difference in the priority of planning units than did the modeling approach used to combine variables into land units. The spatial correlation among soil, geology, and topography appeared to make conservation prioritization fairly robust to the particular variable choice.

Case Study 7: GAP Status and Effects of Decision Rules on Characterization of Geodiversity in the U.S. Southwest

Albano (2015) characterized the geodiversity of the southwestern United States (Arizona, California, Colorado, Nevada, New Mexico, Utah) and assessed the sensitivity of this characterization to different classification methods and spatial scales. To assist land managers with prioritizing places for conservation, a Gap analysis (Scott et al. 1993) was performed to evaluate the degree to which the region's existing PAs network captured geographically diverse places.

Land unit (at 90-m and 270-m resolution) were created based on unique combinations of elevation, topography, and dominant soil suborder (Table 1). Topography was quantified using two indexes derived from a DEM: compound topographic index (CTI) (Moore et al. 1993), an estimate of topographic wetness, and topographic heat load (THL) (McCune & Keon 2002), which integrates

the effects of slope, aspect, and latitude. These variables captured abiotic conditions of importance to plant distributions.

Different land-unit characterizations were developed by varying the classification method used to subdivide each topographic variable (e.g., minimum variance vs. equal subsets, number of divisions in the classification), the spatial resolution at which the topographic variables were derived (90 m vs. 270 m), and the moving window size used to calculate land-unit diversity (window size: 1–23 km²). Within the moving window, land-unit diversity was calculated using Shannon's diversity index averaged across all of the different land-unit classifications. Sensitivity was assessed using analysis of variance, and similarities among the different classifications were assessed using correlation analyses. Gap analysis was used to assess the proportion of protected lands with high land-unit diversity.

Land-unit diversity estimates were slightly more sensitive to moving-window size than to the classification method ($F = 2.49$, $p = 0.11$), but all were highly correlated ($r > 0.88$). Correlations between diversity estimates based on the 90-m versus 270-m resolution data decreased as search area decreased but were still significantly correlated, even at 1 km², the smallest sizes analyzed (average $r = 0.72$).

The protected status of areas with high land-unit diversity varied widely among ecoregions. Soils classified as "miscellaneous areas" and supporting little or no vegetation were the most highly protected soil type (USDA 1993). Areas at intermediate elevations with more productive soil types and high CTI values were relatively less protected, although these environments are more likely to have fine scale climatic diversity and provide refugia for species under a warming climate (Ackerly et al. 2010; Dobrowski 2011).

Albano (2015) concluded that although varying the variable classes, spatial resolution, and moving window size created observable differences among land-unit diversity estimates, results were still highly correlated and thus relatively robust to these decisions. Further, using these data sets to prioritize land for conservation could help identify and correct biases in the current set of protected lands to ensure that they represent all aspects of natural diversity.

Case Study 8: Environmental Diversity Used to Explore Trade-Offs between Conservation and Production in the Southeastern Forests of New South Wales, Australia

Faith et al. (1996) developed a general framework for evaluating trade-offs in systematic conservation planning using a continuous abiotic diversity metric consisting of

geophysical and climatic data as surrogates for overall biodiversity. The results were used to address regional forestry planning issues in the Bateman's Bay region of New South Wales.

The approach used, called "environmental diversity" (ED) (Faith & Walker 1994, 1996), was based on recognizing environmental space as continuous and thus avoided the arbitrary splitting of what is really a continuum of variation among sites. The unimodal response model underlying ED links representation of the environmental space to representation at the species level. Graphically, the number of species represented by a set of sites is large to the extent that, on average, the distance from any point in the environmental space to its nearest PA is small (i.e., the PAs cover all the environmental space). The expected complementarity value of an area, estimated as the relative number of additional species it contributes, is indicated by the extent to which addition of the area to a partial set reduces the sum of these distances.

Twenty-five environmental variables were calculated for 5 primary factors (temperature, precipitation, radiation, nutrient index, and terrain roughness); there were 5 variables for each factor (Faith et al. 1996). Mean monthly temperature, precipitation, and solar radiation values were estimated from latitude, longitude, and elevation in the program ESOCIM (Hutchinson 1984) at the center points of 0.01×0.01 degree grid cells. The resulting 3,439 cells were used as the sites for land-use allocations. Ordination was used to generate an environmental space based on all variables, and distance in ordination space was used as a measure of dissimilarity between grid cells. The 5 primary factors were given equal weight.

We used the DIVERSITY package (Walker & Faith 1994) to derive the allocation of sites to conservation that maximizes total net benefits. Net benefits were based on the estimated number of species captured through the complementarity value of each site in environmental space and the suitability of the site for forestry (Faith & Walker 1994, 1996). Forest suitability costs for each site were calculated based on 47 factors (e.g. distance to saw mill, site productivity). Each area selected for protection had to make a weighted complementarity contribution to biodiversity that exceeds its weighted forest suitability cost.

Faith et al. (1996) argue that the ED measure allowed for the systematic integration of estimated biodiversity consequences into planning efforts that include other preferences for different land uses. The approach avoids arbitrary percentage targets applied to environmental clusters and allows for a more nuanced view of potential trade-offs. This continuous view of biodiversity surrogate information side-steps the problem of first determining a number of types to be counted toward comprehensiveness and then deciding how much heterogeneity within types is to be captured. Weaknesses included the need for better justification of the choice of environmental

variables. Subsequent work developed a combined approach based on biotic and environmental variables and revisited the study to include ecosystem services (Faith 2014).

Discussion

Geodiversity can add new dimensions to conservation planning that augment traditional biodiversity-based approaches and help ensure the lasting conservation of diversity. The case studies show that, in addition to its recognized role as a coarse-filter surrogate for species diversity, geodiversity has also been used to estimate within-ecosystem variation; as a measure of microclimate availability within topographic and elevational gradients; and as a template to assess how well site prioritizations, protected lands, or connectivity models encompass the range of physical and ecological gradients in a region. These functions seem particularly relevant when planning for a different future climate. Moreover, a geophysical approach uses data that are generally available worldwide and is grounded in fundamental concepts of ecology (Lawler et al. 2015 [this issue]). However, the choice of variables, assessment methods, and in particular, the approach to combining variables all have an effect on results and no agreed upon method has yet emerged for designing an effective geophysical template to support diversity into the future.

The degree to which geophysical patterns succeed as surrogates for biodiversity patterns depends in part on the careful selection of geophysical variables. All studies found that distribution patterns of some geodiversity elements, especially soils, elevation, and topography, had high correspondence with the distribution of dominant vegetation types. For instance, Schloss et al. (2011) (case study 4) found that planning units selected to include geodiversity also included most vegetation types (76%), and Buttrick et al. (2014) (case study 5) found that the TNC biodiversity portfolio also captured 91% of the land units that had been calibrated to dominant vegetation patterns. Because the distinctiveness of these geophysical factors is likely to persist under different climates, the utility of using them for developing a conservation plan seems well justified.

The effectiveness of geodiversity in capturing species distributions was generally better for common species than rare ones. Case study 3 suggests that in some regions, bedrock may be more highly correlated with rare species than soil order due to its correspondence with unique environments like serpentine and limestone. The study's high capture of both rare species taxa (75%) and mapped vegetation types (100%) may be because vegetation types are statistically easier to capture in a wide variety of configurations than are rare species, so calibrating geodiversity variables to rare elements should

result in a more species comprehensive portfolio that also captures common vegetation types. However, the high species capture may also be due to additional criteria for local connectedness. Integrating geodiversity with other targets such as rare species locations, vegetation types, or intact landscapes may lead to a more comprehensive template, and the resulting site networks should be more robust to climate change because they incorporate finer-grain ED. Still, some fine-filter conservation targets, like wide-ranging mammals, are unlikely to be tightly linked to geodiversity and will need to be addressed with alternative planning approaches.

Across all studies there were marked similarities in the selection of primary variables, although the exact metric, thresholds, and mapping scale differed substantially. Elevation and slope were the most common topographic variables, and some authors are now experimenting with mapping isobioclimates (Metzger et al. 2013) to reflect orographic effects and better map elevation-related life zones. Case studies 5 and 6 found that strong correlations among many of the geophysical variables made the resulting site networks relatively robust to exact variable choice. The effect of scale was less clear. Case study 3 used explicitly different scales for measuring representation than for measuring micro-climate diversity arguing that these are scale-dependent. However, case study 6 and 7 found that site selection results were highly correlated across scales.

Besides variable choice, characterization of geodiversity requires other subjective decisions that can influence the number of land units and their distribution across a landscape. For example, the method of combining variables had greater effects on the resulting reserve networks than variable choice in 2 studies (6, 7). The overlay method has a strong appeal for conservation use because the resulting units are easy to understand and to locate on the ground. Ecological land units, for example, correspond directly to distinct and recognizable temperature and moisture combinations associated with familiar landforms. In contrast, the statistical *k*-means clustering approach and the ordination methods of Faith et al. (1996) (case study 8) are conceptually appealing because they avoid the artificiality of classification thresholds, are relatively unaffected by correlated variables, and provide a way to minimize within-unit variance in multidimensional space. However, the results are more difficult to interpret. Additionally, cluster methods can be less transparent than overlay methods because several decisions must be made in the cluster process (e.g., similarity metric, clustering algorithm) and the implications of these for site selection are not known. Further, most clustering approaches cannot accommodate a mix of continuous and categorical variables and many are sensitive to outliers.

A common goal of the case studies was to identify a network of representative geophysical stages upon

which communities can transform and develop. To sustain biodiversity, this network must also capture most of the species that will evolve, and have enough spatial coherence and connectivity to maintain ecological processes. Each case study developed a version of such a network, but questions remain about overall spatial design. Case studies 1, 4, 5, and 6 treated the design as an optimization problem and used Marxan to identify the most efficient arrangement of sites that represented all land units. However, a prioritization based on the proportion of runs in which each land unit was in the near optimal solution is not the same as an actual network, which is one of the possible solutions and might look very different spatially. Case studies 3 and 7 prioritized individual sites based on key geodiversity characteristics. These sites are likely of high importance to future biodiversity, but a portfolio based only on high-scoring sites might not have the spatial configuration needed to function as a physical template that sustains all diversity across a region. Three case studies explicitly included connectivity as part of the network (2, 3) or used patch size criteria to get at the area needed for processes such as fire (1).

Research is needed to understand how a coherent geophysical network facilitates function, persistence, and movement under climate change. Collectively the studies suggest four key design steps: define land units based on species-relevant variables combined in an ecologically meaningful way; represent the land units in a logical spatial configuration that integrates species occurrences if possible and review results for ecological coherence; apply selection criteria to individual sites to ensure that they are appropriate for conservation and express desired characteristics (e.g., microclimates or intactness); and evaluate connectivity among sites to maintain movements and ecological processes. With these considerations, conservationists now have an array of tools to design more effective site portfolios incorporating geophysical elements to ensure the lasting conservation of natural diversity.

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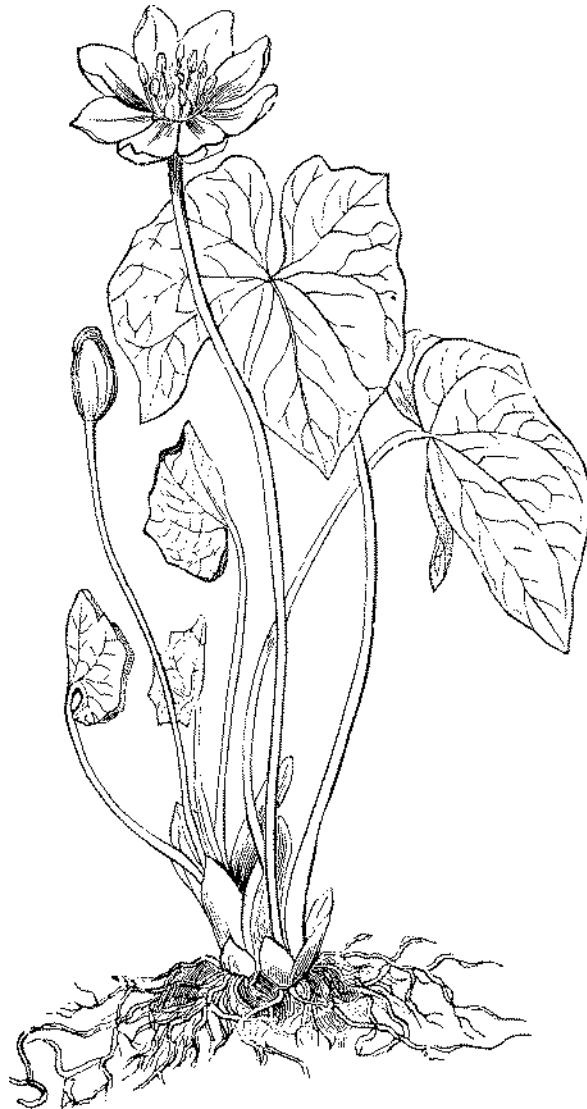
Supporting Information

Additional references for case studies (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.

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Incorporating geodiversity into conservation decisions

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Abstract: *In a rapidly changing climate, conservation practitioners could better use geodiversity in a broad range of conservation decisions. We explored selected avenues through which this integration might improve decision making and organized them within the adaptive management cycle of assessment, planning, implementation, and monitoring. Geodiversity is seldom referenced in predominant environmental law and policy. With most natural resource agencies mandated to conserve certain categories of species, agency personnel are challenged to find ways to practically implement new directives aimed at coping with climate change while retaining their species-centered mandate. Ecoregions and ecological classifications provide clear mechanisms to consider geodiversity in plans or decisions, the inclusion of which will help foster the resilience of conservation to climate change. Methods for biodiversity assessment, such as gap analysis, climate change vulnerability analysis, and ecological process modeling, can readily accommodate inclusion of a geophysical component. We adapted others' approaches for characterizing landscapes along a continuum of climate change vulnerability for the biota they support from resistant, to resilient, to susceptible, and to sensitive and then summarized options for integrating geodiversity into planning in each landscape type. In landscapes that are relatively resistant to climate change, options exist to fully represent geodiversity while ensuring that dynamic ecological processes can change over time. In more susceptible landscapes, strategies aiming to maintain or restore ecosystem resilience and connectivity are paramount. Implementing actions on the ground requires understanding of geophysical constraints on species and an increasingly nimble approach to establishing management and restoration goals. Because decisions that are implemented today will be revisited and amended into the future, increasingly sophisticated forms of monitoring and adaptation will be required to ensure that conservation efforts fully consider the value of geodiversity for supporting biodiversity in the face of a changing climate.*

Keywords: abiotic diversity, adaptive management, conservation planning, conservation policy, ecological diversity

Incorporación de la Geodiversidad en las Decisiones de Conservación

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Resumen: *En un clima que cambia rápidamente, quienes practican la conservación podrían usar la geodiversidad de mejor manera en una gama amplia de decisiones de conservación. Exploramos vías selectas por medio de las cuales esta integración puede mejorar la toma de decisiones y las organizamos dentro del ciclo de manejo adaptativo de evaluación, planeación, implementación y monitoreo. En pocas ocasiones se menciona a la geodiversidad en las leyes y la política ambiental predominantes. Como la mayoría de las agencias de recursos naturales bajo mandato de conservar ciertas categorías de especies, el personal de las agencias se ve enfrentado a encontrar formas de implementar de manera práctica nuevas directivas con miras a salir adelante frente al cambio climático mientras se retienen los mandatos centrados en especies. Las ecoregiones y las clasificaciones ecológicas proporcionan mecanismos claros para considerar a la geodiversidad en los planes o decisiones. Esta inclusión ayudará a fomentar la resiliencia de la conservación ante el cambio climático. Los métodos para la evaluación de la biodiversidad, como el análisis de intervalo, el análisis de vulnerabilidad ante el cambio climático, y el modelado de procesos ecológicos, pueden adaptarse pronto a la inclusión del componente geofísico. Adaptamos las estrategias de otros para caracterizar paisajes de resistente, a resiliente, a susceptible, y hasta sensible, a lo largo de un continuo de vulnerabilidad ante el cambio climático de la biota que presentan y después resumimos las opciones para integrar a la geodiversidad en la planeación en cada tipo de paisaje. En los paisajes que son relativamente resistentes al cambio climático, existen opciones para representar completamente a la geodiversidad mientras se asegura que los procesos ecológicos dinámicos pueden cambiar a lo largo del tiempo. En los paisajes más susceptibles, las estrategias que buscan mantener o restaurar la resiliencia ambiental y la conectividad son primordiales. Implementar acciones sobre el suelo requiere del entendimiento de las restricciones geofísicas sobre las especies y un enfoque cada vez más ágil para establecer objetivos de manejo y restauración. Ya que las decisiones que se implementan hoy en día serán reconsideradas y modificadas hacia el futuro, se requerirán de formas de monitoreo y adaptación cada vez más sofisticadas para asegurar que los esfuerzos de conservación consideren de lleno el valor de la geodiversidad para apoyar a la biodiversidad de frente al clima cambiante.*

Palabras Clave: diversidad abiótica, diversidad ecológica, manejo adaptativo, planeación de la conservación, política de conservación

Introduction

Why Geodiversity is Important to Conservation

The challenge posed by climate change in the coming decades is to clarify and implement the conservation strategies that best strengthen ecosystem resilience and minimize ecological degradation or collapse and then to facilitate the transformation of ecosystems in ways that maximize retention of species and their interactions. Because conservation practitioners have not previously experienced a period of rapid climate change, management responses to such a challenge are necessarily working hypotheses (Fischer et al. 2009). Given the likely importance of interventions to mitigate adverse effects on biodiversity, conservation decisions must be based on fundamental ecological principles and approaches that facilitate our coping with unforeseeable surprises (Staudinger et al. 2013).

Abiotic diversity has long been thought to play an important role in fostering and maintaining biodiversity (Lawler et al. 2015 [this issue]). As in G.E. Hutchinson's metaphor of the "ecological theater" (Hutchinson 1965), the geophysical setting and climate have provided "the stage" for the many actors in the "ecological and evolutionary play." Geodiversity is indeed a significant driver of the distribution of biota. The greater the breadth of

environmental conditions, the more niche space there is for species to occupy or differentiate within and, hence, the higher the total biological diversity the environment can support. The conservation corollary to this is that unless we conserve a fully representative cross-section of environments, in all likelihood, we will lose some elements of associated biota (Scott et al. 2001; Aycrigg et al. 2013).

Climate change adds to the importance of conserving diverse niche space. In periods of climate change, species move independently of each other and sometimes in counter-intuitive ways. Conserving a wide array of geophysical settings, with associated ecological processes, can not only preserve the places occupied by species today, but also preserve places that may be occupied as ecosystems transform in the future.

We focus here on some practical issues regarding the integration of geodiversity into conservation decision making. We first provide contextual background on natural resource policy. We then highlight selected avenues where this integration might improve conservation decisions, organized within an adaptive management cycle. We use the term *geodiversity* to refer to settings defined by soil and topography, *abiotic diversity* for the union of geodiversity and climate diversity, and *ecological diversity* for the combination of biotic and abiotic factors.

Addressing Geodiversity in Natural Resource Law and Policy

Natural resource laws originated to regulate exploitation of land and water resources, protect or enhance environmental quality, or provide consumptive ecosystem services. Generally, geodiversity has been addressed only indirectly in public policies related to these laws. For example, in law and policy aiming to protect wilderness or scenic values, geodiversity is among the values being conserved. Although these policies are not specifically aimed at capturing the full cross section of geodiversity, in many cases, extraordinary geophysical features have gained protective status under these policies and programs, such as National Natural Landmarks (U.S.A.), Sites of Special Scientific Interest (U.K.), and Global Geoparks Network (UNESCO). Other examples come from clean water policy. In the United States and Australia, water management regulations increasingly recognize the importance of geophysical aspects of floodplains related to surface water storage, linkages to recharge, and basin flow regulation (Water Act 2007; Hough & Robertson 2009).

More often in natural resource policy, geodiversity is treated as a component of broader concepts such as ecological diversity that combine abiotic and biotic factors. For example, as law and policy governing renewable natural resources expanded from regulating hunting and fishing to species survival (e.g., U.S. Endangered Species Act of 1973 [ESA]), references to ecological diversity emerged (Freyfogle & Goble 2009). In one specific case, the U.S. Fish and Wildlife Service's ecosystem approach addresses circumstances where numerous species could be listed under ESA due to their shared dependence on similar threatened habitats. Internationally, signatories to the Convention on Biological Diversity adopted a focus on ecological diversity through the Aichi 2020 targets (CBD 2011). Target 5 (reduce the rate of habitat loss) and target 11 (ensure sufficient ecological representation among protected lands and waters) are both opportunities to more specifically integrate geodiversity into biodiversity conservation.

Policy governing management of U.S. National Forests provides another example of the role of ecological diversity in decision making. In emphasizing the maintenance of ecological integrity, the 2012 planning rule directs planners to take into account "system drivers, including dominant ecological processes, disturbance regimes, and stressors, such as natural succession, wildland fire, invasive species, and climate change; and the ability of terrestrial and aquatic ecosystems in the plan area to adapt to change" (Department of Agriculture Forest Service 2012).

The U.S. National Fish, Wildlife, and Plants Climate Adaptation Strategy (National Fish, Wildlife, and Plants Climate Adaptation Partnership 2012), co-led by the U.S. Fish and Wildlife Service, the National Oceanic and Atmospheric Administration, and the states, highlights the

importance of geodiversity in its very first recommended action: "Identify and map priority areas for conservation using information such as . . . geophysical settings" The strategy also highlights the importance of a strategy to "conserve, restore, and . . . establish new ecological connections among conservation areas to facilitate fish, wildlife, and plant migration, range shifts, and other transitions caused by climate change."

We see numerous opportunities under existing policy to better integrate geodiversity into conservation decision making. But this integration will likely require agencies to consider whether practical approaches to conserve geodiversity can support and complement their core species-centered mandates.

Conservation decisions have an inherent temporal dimension. One must ask: Within what time frame is the action from this decision intended to apply? Is it intended to stand in perpetuity, the next 100 years, or the next 10 years? Given uncertainties inherent in ecosystem-based decision making and the accelerating rate of landscape change (in both climate and land use), an increasingly iterative, adaptive approach is required (O'Connor et al. 2012). Adaptive management in conservation has been articulated in a number of ways with all approaches include a repeating cycle of evaluation or assessment, followed by planning or prioritization, implementation, and monitoring (Williams et al. 2009). Assessment involves the periodic appraisal of conditions and trends to determine if there are needs for change. Planning acts on those needs, typically constructing alternatives, prioritizing resource allocations, and establishing time frames for action. Implementation involves applying those specified actions on the ground (Pressey et al. 2013). Monitoring involves the ongoing measurement of actions and outcomes in order to maximize success and minimize uncertainty over time.

We focus here on conservation decisions typically applied at two spatial scales. Some decisions, often implemented at regional scales, involve selection of places in need of action. Other decisions, often applied at a more local scale, establish the strategies and actions best suited to conserving the selected places.

The following discussion includes examples of opportunities to advance conservation with geodiversity organized along the major phases of the adaptive management cycle of assessment, planning, implementation, and monitoring.

Using Geodiversity in Ecological Assessment

ECOREGIONS AS ANALYSIS AREAS FOR ASSESSMENT AND PRIORITIZATION

Regional patterns of abiotic diversity underlie the definition of ecoregions around the world. Ecoregional delineations have become well established across ecological

realms (Olsen et al. 2001; Spaulding et al. 2007; Abell et al. 2008) at continental scales (Commission for Economic Cooperation 1997), national scales (Ecoregions Working Group 1989), and regional scales (Ravichandran et al. 1996). These are often structured as spatially nested hierarchies defining land- or water-scapes of increasing homogeneity at lower levels, based on climate, physiography, landform, hydrology, soil, and other factors (Bailey 2009). The middle levels of these hierarchies have been used widely, substituting for political jurisdictions, to define the analysis area for assessment, and selecting priority areas at regional scales (Groves 2003).

FOCAL CONSERVATION TARGETS WITHIN ECOREGIONS

Within ecoregions, adaptive decision making typically starts by answering some key questions such as: What do we want to conserve? Where is it? What are the major trends in its extent, integrity, and vulnerability? How much is already well conserved? Despite advances in species conservation (Caro 2010), conserving complex ecosystems is facilitated by a pragmatic and complementary coarse-filter to the species-based fine filter. Even ignoring climate change, an ecological coarse filter provides for both the ability to treat simultaneously many species that share similar habitat requirements while also addressing many other far more numerous species for which little is known (Noss 1987). The combined coarse-filter and fine-filter approach to conservation planning is commonly applied in widely varying circumstances. Fortunately, there are expanding opportunities to integrate geodiversity into these multi-scalar approaches to conserve biodiversity.

ECOLOGICAL CLASSIFICATIONS

Substantial investments in ecological classification and mapping could be better utilized to integrate geodiversity into conservation decision making. Classification of ecosystems is analogous to species taxonomy and allows for a practical categorization and description of types (Walter 2002). Ecosystem classification facilitates communication and the systematic accumulation of knowledge.

Classifications take a variety of forms, depending on the original intent of their developers. In terrestrial environments, classifications commonly focus on vegetation (Specht & Specht 1999; FGDC 2008). In forestry and rangeland management, a common motivation is to predict biomass productivity and other conditions of a given site, so these classifications emphasize geophysical characteristics such as microclimate, landform, drainage, and soil properties (USDA Forest Service 2001; Caudle et al. 2013). Historically, this was common in regions with a long history of intensive human land use and where few examples of natural vegetation were available for study

(Barnes 1996). Similarly, some approaches to wetland classification are based entirely on geomorphology and hydrologic regime (Brinson 1993). In aquatic environments, ecological classifications have a much more limited history, but they also tend to emphasize geophysical attributes (hydrologic regime, water chemistry) in type definition (Higgins et al. 2005; FGDC 2012). For example, under the Ramsar Convention, aquatic types are defined in terms of marine versus inland environments and then subdivided primarily by hydrologic regime, salinity gradients, and soil properties.

But in many cases, terrestrial classifications integrate biotic and abiotic characteristics (e.g., Holdridge 1947; Pojar et al. 1987). The commonly used wetland classification standard in the United States (Cowardin et al. 1979) defines wetlands using substrate, flooding regime, and vegetative life forms. Recent advances in remote sensing and spatial modeling and the understanding of abiotic drivers of vegetation structure and composition (Palik et al. 2000) have enabled classification units to be mapped at increasingly fine resolution (Lowry et al. 2007). These classifications and maps may represent geodiversity quite directly with units such as sand dunes, desert playas, desert or alvar pavements, cliffs, canyons, or alpine scree (Comer & Schulz 2007) because those geophysical settings quite directly express patterns in biotic composition and ecological process.

Many ecological classifications are structured hierarchically from broad (heterogeneous) to fine (more homogeneous) (UNESCO 1973; Grunblatt et al. 1989). For example, the U.S. federal vegetation classification standard (FGDC 2008)—primarily a biotic classification—describes units at eight levels. At the level of vegetation formation (level 3) Tropical Dry Forest is one classification unit, encompassing the climatic and compositional variability of all dry forests in tropical latitudes. Realistically, these heterogeneous species assemblages persisted for millennia. In contrast, individual forest plant associations (level 8) are defined by the composition of diagnostic species at each level of the forest canopy. When fully developed worldwide, there would likely be hundreds of associations within the Tropical Dry Forest formation, each encompassing a much narrower range of climate variability.

As climate changes, classification schemes that describe units narrowly in terms of biotic composition, structure, and dynamics may not persist (Landres et al. 1999), and these would tend to be units defined at lower levels of a classification hierarchy. But these limitations are much reduced in the context of near-term decisions and more broadly defined classification units because the range of ecological heterogeneity within units is wider relative to the likely climate-change effect within that shorter timeframe. Therefore, users of existing ecological classifications must consider the degree of climate change projected for the area of interest; the time frame

intended for the conservation decision; and the relative climatic and compositional heterogeneity described by a classification unit.

TARGETING GEOPHYSICAL PATTERN AND PROCESS

Others have highlighted the importance of conserving geodiversity, either as the foundation for key ecosystem services or for its own sake (Gray 2013; Hjort et al. 2015 [this issue]). Although unusual geological features have been the focus of individual conservation efforts (e.g., the geothermal features of Yellowstone National Park in the United States), few areas have been protected specifically for geodiversity. The non-governmental organization UKGAP (www.ukgap.org.uk) provides one example of an established action plan with measurable indicators for progress at identifying and securing geodiversity. Key activities include documenting the location and condition of geologic features, raising awareness of the importance of their conservation, and developing adaptive management plans in local sites (Prosser et al. 2010). A systematic focus on representative geological patterns and processes can ensure that the geodiversity of a given region or site is appropriately conserved.

Gap analysis (*sensu* Scott et al. 1993) can be used to document which geophysical or land facet types (*sensu* Wessels et al. 1999) or at-risk soil types (Tennesen 2014) are already sufficiently protected and which need additional attention. Because no single level of representation is guaranteed to secure geodiversity and biodiversity, one can explore conservation scenarios based on varying levels of representation for each land facet type (Anderson et al. 2015 [this issue]).

The geological processes of greatest interest to conservation are typically those occurring in relatively short time frames, such as coastal sediment movements and dune dynamics, dynamics of sediment on river floodplains, montane avalanche chutes, karst-related hydrodynamics, and glacial movement. These geophysical dynamics maintain ecological patch dynamics that many species rely upon, and many are also threatened by human alterations in short-time scales.

ASSESSMENT OF ECOLOGICAL PROCESSES

If geodiversity provides the stage, one could argue that ecological processes—most driven by abiotic diversity—determine many changes in sets and scenes. A common concern in conservation assessment is for the relative intactness of key ecological processes that support biodiversity in a given area. For example, are hydrologic flow regimes or natural wildfire regimes occurring? How might these ecological processes be changing with climate change? Are there ecological process thresholds where transformation to a novel assemblage of species may result (Briske et al. 2006)?

In many cases, ecological classification units, be they based on geophysical setting, biotic assemblage, or some combination, form the basis for modeling ecological processes. Conceptual state-and-transition models have been used increasingly to describe disturbance and biotic response for a given geophysical setting (Bestelmeyer et al. 2004; Cale & Allen-Diaz 2009). A given state might be defined as the characteristic composition and structural attributes at one point along one or more successional pathways, while transitions describe the successional or disturbance processes among states. Rumpff et al. (2011) illustrate the use of these models for adaptive restoration of native woodlands in Australia. The process model allowed managers to articulate assumptions about vegetation dynamics and interactions with restorative practices. Monitoring effects of the practices allowed for effective learning and updated models to better predict restoration outcomes. Within the United States, land management agencies such as the Natural Resources Conservation Service have supported development of conceptual process models based on ecological site classification units that are each defined in terms of geophysical characteristics, such as landform, drainage, and soil properties (Caudle et al. 2013). Similar models have been developed for hundreds of biophysical settings across the United States through the inter-agency LANDFIRE effort (Rollins 2009). Planners and managers use these models to make both strategic and tactical decisions regarding wildfire and vegetation management. This type of assessment is increasingly being summarized at regional and national scales, providing insights for broad-scale planning and policy makers (Swaty et al. 2011).

In aquatic ecosystems, parallel approaches have emphasized use of geophysical setting and hydrologic regime to organize the description of reference conditions, measurable from samples of aquatic biota (Hawkins et al. 2010). Again, field sampling and remotely sensed measurements can be used to compare observed vs. expected values to assess the degree to which conditions have been altered or are changing over time.

With accelerating landscape change over the coming decades, these methods for assessment should assist with determining, for a given geophysical setting, the rate at which the cast of actors could in fact be turning over and the degree to which that turnover is an effect of climate change or from other causes.

ASSESSING CLIMATE CHANGE VULNERABILITY

Climate change vulnerability assessment is increasingly being conducted at the scales of landscapes and ecoregions (Beaumont et al. 2011). One can initially categorize a given ecoregion (1000s of km²) or component landscape (100s of km²) in terms of potential climate-change vulnerability for the biota it supports. We took some inspiration from Gillson et al. (2013) to categorize

Table 1. Relative vulnerability to climate change resulting from various combinations of a landscape's geodiversity, ecological intactness, and landscape connectivity.*

	<i>Ecological intactness and landscape connectivity (assumed to be mutually correlated)</i>		
	<i>low</i>	<i>moderate</i>	<i>high</i>
Low geodiversity	sensitive	susceptible	susceptible
High geodiversity	resilient	resilient	resistant

*Different management activities are appropriate to each of the 4 levels of vulnerability (see text).

a given area for climate-change vulnerability based mainly on physical characteristics that affect the ability of species to persist during climate change. This generalized categorization is adapted and summarized here in Table 1. Resistant areas have characteristics conferring inherent adaptive capacity to the biota it supports, including high-topographic variability, ecological intactness, and landscape connectivity. Topographic variability provides, in effect, a diversity of microclimates within close proximity, including microclimates that are decoupled from regional climate (Dobrowski 2011). Ecological intactness provides a diversity of species and ecological processes characteristic of the area. Landscape connectivity provides options of species to move long distances. At the opposite extreme are landscapes categorized as sensitive that lack all of these characteristics. Resilient landscapes have high-topographic diversity but may have histories of land use resulting in diminished ecological intactness and landscape connectivity. Susceptible landscapes have moderate to high-ecological intactness or landscape, but low topographic diversity.

Once categorized, these four generalized conditions, resistant, resilient, susceptible, and sensitive, suggest different sets of adaptation strategies (Heller & Zavaleta 2009; Mawdsley et al. 2009), each involving the conservation of geodiversity, as described in the next section.

Using Geodiversity in Planning Conservation Actions

Systematic approaches linking assessment to planning involve answering questions such as: How much more requires conservation? Where might we best complement current investments? What specific actions are needed? The answers to these questions may differ depending on the relative vulnerability of the landscapes to climate change.

Resistant landscapes already incorporate high geodiversity, so wait-and-watch strategies are appropriate to detect anticipated change among sensitive species and ecological processes. Conservation actions here secure the high level of intactness and connectivity, especially

if they face imminent or future threats from human activities.

In resilient landscapes, strategies aim to minimize likely negative effects of climate change. High-topographic diversity enhances potential resilience because species there are more likely to have both space and time to move to nearby locations retaining suitable habitat conditions as climatic envelopes shift. However, past and current uses of land and water may have resulted in habitat fragmentation and degradation to many component ecosystems and species, both of which are needed to increase connectivity and potential for range shifts.

Large portions of the North American Rocky Mountains or Andes of South America provide examples of relatively resilient landscape conditions. In these areas, especially where there are extensive public lands, or are otherwise sparsely populated, rugged montane physiography naturally encompasses high geodiversity with relatively high proportions of natural land cover. Planning approaches can build on current investments to secure the full range of geodiversity within conservation lands, and then concentrate on the restoration of ecological intactness and connectivity where degradation has occurred. Methods well suited to these circumstances, include those of Neely et al. (2001) aiming to ensure that ecological diversity is sufficiently represented within priority conservation areas. That effort also utilized ecological process models to better understand natural disturbance dynamics and then imposed minimum patch size and overall extent goals with reserve selection algorithms.

Beier (2012) provides practical recommendations for connectivity design in these circumstances, with linkages designed around riparian zones and across climate gradients, and short connections across areas of greatest topographic diversity. Theobald et al. (2012) also provide methods for spatially modeling overall landscape permeability that should assist with targeting investments across a given regional matrix.

Conservation actions within selected areas can then emphasize the maintenance of composition and structure close to what might occur today or what might be predicted to occur over upcoming decades. Removal of invasive species likely remains a feasible strategy because native species recolonization from surroundings is more likely and this strategy limits at least some risk from the unpredictable behavior of invasives. Natural disturbance regimes that have been previously altered in these areas can also be feasibly addressed but should anticipate climate-induced effects. Examples include the emerging interaction of past fire suppression, warming climate, insect outbreak, and fire patch size in the US Rocky Mountains (Kulakowski et al. 2012). In these areas, the key will be to retain sufficient contiguous area to allow for natural disturbance regimes such as wildfire to change as climate changes.

In susceptible landscapes, limited topographic diversity may result in rapid horizontal changes in climatic conditions, perhaps too fast for some species to match, with rapid change in species composition and transformation of extant ecosystems (Loarie et al. 2009). Examples of these landscapes in the Americas include lowland ecoregions of North and South America, such as those in the Atlantic and Gulf Coastal Plain in the United States and the Chaco and Cerrado of Paraguay and Brazil. Garcia et al. (2014), in their global analysis of potential climate change metrics, indicate the potential for high-climate change velocities throughout polar regions and in the tropical regions of central Africa, the western Amazon, and in southern Australia. In these areas, relatively flat physiography naturally encompasses limited geodiversity. Strategies therefore aim to better represent ecological diversity within conservation lands and to secure the capacity to cope with the effects of climate change by ensuring that critical ecological processes are maintained or restored to a high level of function.

Approaches to conservation in susceptible landscapes might be grouped into those primarily treating ecological diversity (i.e., both biotic and abiotic components) versus those primarily centered on geodiversity (Anderson et al. 2015). Methods centered on geodiversity are well suited to landscapes where biodiversity data are very limited or lacking, but sufficient geographic data exist to characterize geodiversity and relative landscape intactness (Beier & Brost 2010). Examples of these methods from Anderson et al. (2015) emphasize use of geology and local geomorphology to map geodiversity. In relatively fragmented regions, design is sometimes directed toward identifying relatively large and intact patches that maximize representation of geodiversity, but it can also highlight remaining fragments in heavily used landscapes that provide the last opportunities to protect some ecosystems (Cowling et al. 2003), even if these are likely to look different under climate change. In more arid regions, options to maximize drought refugia should be explored (Klein et al. 2009).

In these landscapes, because of the rapid rate of climate-induced change on species habitats, there is an urgent need to secure landscape connectivity. At regional scales, maximizing linkages among landscape blocks and enhancing permeability of the between-block matrix would maximize opportunity for species movement and minimize disruption to key ecological processes (Rudnick et al. 2012), even though this comes at increased risk of facilitating expansion of invasive species (Dukes & Mooney 1999). Rouget et al. (2003), Brost and Beier (2012), and Nuñez et al. (2013) provide practical approaches to support regional connectivity aimed at facilitating climate change-induced movements while meeting other conservation goals.

Sensitive landscapes may require intensive management interventions focused on component ecosystems

and species, especially where endemic species are at stake. Abating key non-climate stressors (e.g., altered ecological processes) will tend to be most costly here due to the cumulative effects of multiple stressors and species extirpations. These are also areas where the need for managed translocation or assisted colonization are most likely (McLachlan et al. 2007). One can anticipate that transformations to novel ecosystems will be concentrated in these landscapes, so strategies may center on conserving representative geodiversity and restoring key ecosystem functions and services (Jackson & Hobbs 2009).

Managing Toward Resilience

Within the adaptive management cycle, planning and strategy translates into specific actions implemented on the ground, often including planting, harvesting, or otherwise treating vegetation, and these actions can incorporate geodiversity into day-to-day decisions. Variation within and across some ecosystem types is often highly predictable by geomorphic and soil variables and should be incorporated into restoration and stewardship goals (Palik et al. 2000). For example, in landscapes with relatively low topographic relief, small differences in elevation may result in a large response by vegetation and must be considered in restoration. In the lower Mississippi alluvial valley of the United States, afforestation efforts have often failed due to the inappropriate selection of tree species for planting given the hydrologic site conditions. The well-drained sites have the highest potential for biomass productivity, and as a result, these sites have largely been converted to agriculture. Regional restoration strategies for bottomlands have therefore incorporated these better-drained sites in spatial prioritization (Tweltdt et al. 2006).

However, given a changing climate, one must add to this site-based knowledge the consideration of climate exposure at the site and the foreseeable timing of that exposure. This is essential to select species for restoration plantings and establish appropriate conservation and restoration targets. Species that may be suitable to climate conditions 50 years into the future cannot be planted until then.

Monitoring Environmental Change

Through monitoring, we find out if we have implemented what we planned and if those actions had the desired effect. Climate change brings increased urgency to invest in effective monitoring of ecosystem change in order to support a timely response. Hierarchical frameworks (Noss 1990) and ecological stratification based on abiotic diversity (Metzger et al. 2013) provide an initial top-down structure for organizing monitoring. What indicators should be included in monitoring networks? As referenced throughout this paper, numerous aspects of

ecological diversity are likely candidates to be monitored and reported on from local to continental scales. These include key aspects of the changing climate, as well as geophysical processes supporting the maintained of biodiversity. One can expect that interactions between climate and ecosystem dynamics, such as wildfire and flooding regimes, will continue to change in an unprecedented manner. The biotic response to these changes, as well as their interactions and feedbacks, should be a strong focus of environmental monitoring.

Conclusions

Given its significance to ecological and evolutionary processes and outcomes and its foundational contributions to ecosystem services and human well-being, the conservation of geodiversity should be better acknowledged and supported in law and policy. Where geodiversity defines the stage and abiotic diversity defines both the stage and set, ecological diversity acts with these, bringing a continually changing cast of actors. Conservation decisions apply to the unfolding reality of the drama on the ground, so it is critical that these decisions consider all of these components as global change accelerates.

While existing approaches to manage dynamic ecosystems have notable strengths and weaknesses, climate change adds urgency to apply adaptive approaches to decision making about where, when, and how we make conservation investments. Increasingly, sophisticated forms of adaptive management will be required to ensure that strategies and plans take full advantage of geodiversity.

Acknowledgments

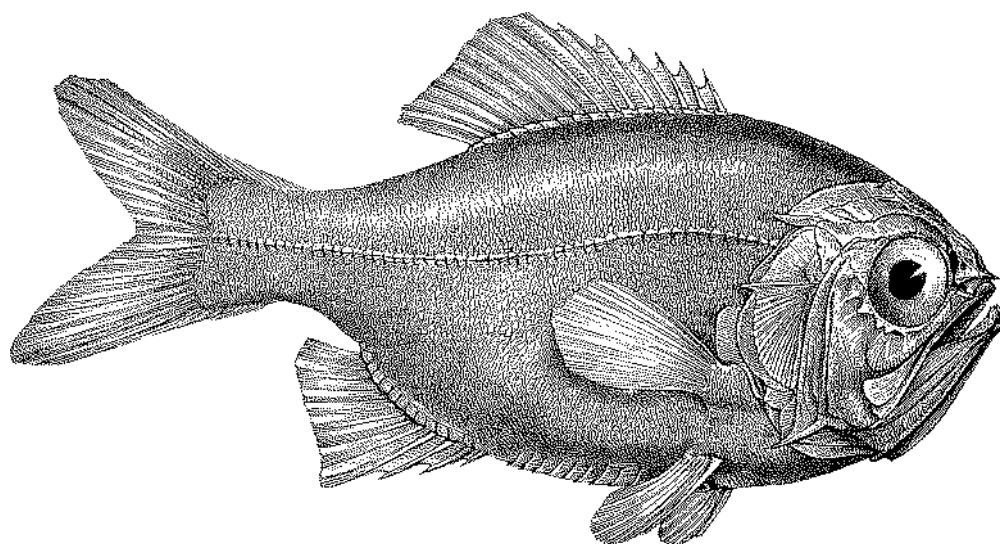
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Cover: Limestone pavement in Iser, France. The calcium-rich environment of limestone pavement, a type of geosite, has little soil but supports specialized species, from lichens to ground-nesting birds. Enduring geophysical features, such as topography, soil, rocks, and water, form the stage on which nature's play is enacted and can be used to prioritize sites for conservation. Conserving nature's stage is a promising basis for maintaining biodiversity where data on species are lacking and offers an approach to conservation under climate change that avoids precarious climate models. See Special Section: Conservation Nature's Stage (pages 613–617).

Photographer: A former biologist, now wildlife and conservation photographer, Denis Palanque (denispalanque.com) has years of experience working with environmental and scientific projects. He strives to be both an artist and a scientist. This blend reflects the spirit of his work with organizations such as *National Geographic Magazine* (French edition), regional natural parks in France, museums of natural history, and conservation organizations. Lately, he has worked in South America for National Geographic - France on a story that reports on the quest for venom for pharmaceutical use, work that illustrates how the future of humans still depends on nature's resources. Currently he is working on a conservation story in South Africa on the issue of human and predator cohabitation: Au Coeur du the Karoo Predator Project (<https://www.facebook.com/AuCoeurduKaroo>).

Use of this issue's cover photograph is made possible by a partnership between the Society for Conservation Biology and the International League of Conservation Photographers (ConservationPhotographers.org). The mission of iLCP is to translate conservation science into compelling visual messages targeted to specific audiences. The iLCP works with leading scientists, policy makers, government leaders, and conservation groups to produce the highest quality documentary images of both the beauty and wonder of the natural world and the challenges facing it. The members of iLCP have proven a commitment to conservation action, superior photographic skills, and the highest ethical standards.

