



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*

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 individualistically 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 oxbow 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 paleo-tempests 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 geomorphic change, are available at broader spatial and temporal

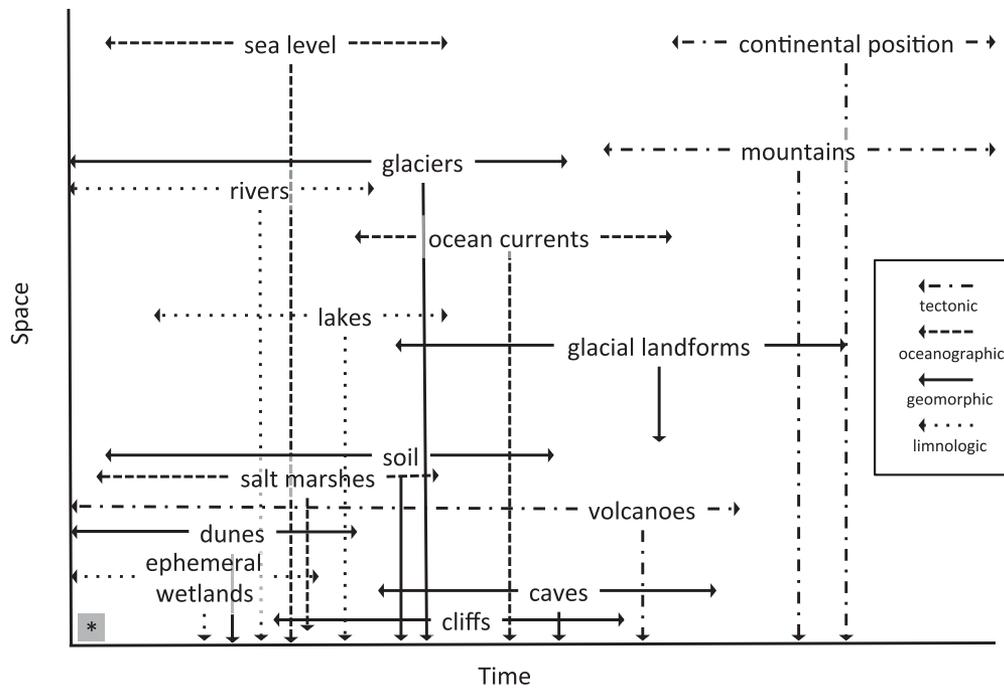


Figure 1. Durability of select landforms (dashed arrows, range of spatiotemporal durability of land facets; box with an asterisk, spatiotemporal scale of typical ecology and conservation research).

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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