

The rise of novelty in ecosystems

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Abstract. Rapid and ongoing change creates novelty in ecosystems everywhere, both when comparing contemporary systems to their historical baselines, and predicted future systems to the present. However, the level of novelty varies greatly among places. Here we propose a formal and quantifiable definition of abiotic and biotic novelty in ecosystems, map abiotic novelty globally, and discuss the implications of novelty for the science of ecology and for biodiversity conservation. We define novelty as the degree of dissimilarity of a system, measured in one or more dimensions relative to a reference baseline, usually defined as either the present or a time window in the past. In this conceptualization, novelty varies in degree, it is multidimensional, can be measured, and requires a temporal and spatial reference. This definition moves beyond prior categorical definitions of novel ecosystems, and does not include human agency, self-perpetuation, or irreversibility as criteria. Our global assessment of novelty was based on abiotic factors (temperature, precipitation, and nitrogen deposition) plus human population, and shows that there are already large areas with high novelty today relative to the early 20th century, and that there will even be more such areas by 2050. Interestingly, the places that are most novel are often not the places where absolute changes are largest; highlighting that novelty is inherently different from change. For the ecological sciences, highly novel ecosystems present new opportunities to test ecological theories, but also challenge the predictive ability of ecological models and their validation. For biodiversity conservation, increasing novelty presents some opportunities, but largely challenges. Conservation action is necessary along the entire continuum of novelty, by redoubling efforts to protect areas where novelty is low, identifying conservation opportunities where novelty is high, developing flexible yet strong regulations and policies, and establishing long-term experiments to test management approaches. Meeting the challenge of novelty will require advances in the science of ecology, and new and creative conservation approaches.

Key words: *Anthropocene; biodiversity; Centennial Paper; conservation; global change; no-analog; novel climates; novel ecosystems; novelty.*

INTRODUCTION

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I've a feeling we're not in Kansas anymore.

—Dorothy, The Wizard of Oz

The world is changing fast, and many places are moving into uncharted territory. Since the founding of the Ecological Society of America, 100 years ago, global

human population has tripled (United Nations Population Division 1999), atmospheric CO₂ has increased by 25% (Ciais et al. 2013), and extinction rates are now approximately 1000 times higher than geological background (Pimm et al. 2014). In the future, rates of these changes and many others, such as species invasions, nitrogen deposition, and climate change, may rise even more. One expected result of these changes is the emergence of abiotic and biotic conditions that are outside the historical range of variability of a given place (Mora et al. 2013), and sometimes without analog anywhere on the planet either today or in the past (Williams and Jackson 2007). In other words, many ecosystems and places are not just changing, but they are also becoming increasingly novel.

Paleoecology, biogeography, and restoration ecology have grappled with the issue of novelty. Paleoecology and biogeography have focused on rising novelty in species associations due to the individualistic responses of species to climate change (Williams and Jackson 2007, Garcia et al. 2014). As novelty rises in abiotic conditions, such as climate, species are expected to reshuffle into novel associations, as they have in the past (Jackson and Overpeck 2000, Williams and Jackson 2007). Restoration ecology has focused on the contemporary rise of “novel ecosystems,” typically stemming from introduced species and the legacies of land use (Lugo and Helmer 2004, Hobbs et al. 2006, 2009, 2013), and resulting changes in the biotic composition relative to a historical baseline (Lugo and Helmer 2004, Cramer et al. 2008, Lugo 2009).

Defining novel ecosystems categorically in a way that clearly differentiates them from non-novel ecosystems has proven to be difficult (Hobbs et al. 2013, Kueffer 2014, Morse et al. 2014). Proposed criteria include human agency as the critical trigger (Hobbs et al. 2006) and self-perpetuation after passing a threshold beyond which it is impossible to restore novel ecosystems (unlike “hybrid ecosystems” that can be restored back to a historical state [Hobbs et al. 2006, 2009]). These definitions of novel ecosystems have received substantial pushback on multiple grounds (Murcia et al. 2014). Some criteria, such as self-perpetuation, are very hard to identify, while the ability to restore a system may depend more on available management resources rather than on intrinsic properties of the ecosystem itself. At a more fundamental level, the underlying conflict is whether novel ecosystems represent the “new ecological world order” and an opportunity for conservation and natural resource management that should be embraced (Hobbs et al. 2006), or if the entire concept of novel ecosystems is nothing more than a “Get-Out-of-Jail-Free Card” for companies, a “Trojan horse” for conservation with dangerous implications for conservation policy and action (Simberloff et al. 2015).

Although the conceptualization of novel ecosystems as currently put forward has limitations, there is ample evidence for novelty in ecosystems. Species invasions

and land use have pushed the species composition of many ecosystems to highly novel states relative to historical baselines, and climate change, shifts in nutrient cycling, and other environmental changes are moving the abiotic conditions of many ecosystems to highly novel states as well (see *The rise of novelty in ecosystems: Case studies*). We suggest that attempts to separate novel ecosystems categorically from those that are not are bound to fail. We argue that the rise of novelty in ecosystems is pervasive but occurs along a continuum, with some ecosystems more novel than others. This conceptual framework lends itself well to dissimilarity-based quantitative frameworks to measure novelty in multiple environmental and anthropogenic dimensions of current and future novelty (see *Global mapping*). We do not use human agency as a criterion for novelty because the effects of human agency on contemporary ecosystems are now so pervasive that there is no meaningful way to identify ecosystems lacking any human touch (Cronon 1995), and novelty in species composition is the expected response to any large-scale environmental change, even in the absence of human activity (Lugo 2013). However, human agency is certainly one, if not *the*, major driver of the rise of novelty today.

We define novelty as the degree of dissimilarity of a system, measured in one or more dimensions relative to a reference baseline, usually defined as either the present or a time window in the past. Defining novelty requires specifying a reference baseline and the dimensions of interest. This means novelty exists along a continuum, and while it is pervasive, it is much higher in some places than others. Novelty occurs in multiple dimensions, both abiotic and biotic. For example, abiotic novelty can result from changes in climate, atmospheric nitrogen deposition, or the environmental changes associated with greater human population density. Biotic novelty can result from changes in species composition, structure, or ecological processes. Abiotic novelty can cause biotic novelty (Chapin and Starfield 1997, Williams and Jackson 2007, Bogan and Lytle 2011, Correa-Metrio et al. 2012), but the extent to which this happens is system- and process-specific. At the same time, biotic novelty can occur without abiotic novelty, e.g., a nonnative species introduction may create novelty in species composition while abiotic conditions remain essentially unchanged. Hence, rigorously measuring novelty requires explicit definition of the relevant variables.

Novelty is distinct from change, and places that change the most are not necessarily the most novel. For example, temperature increases over the past century have been highest in the Arctic. However, the Arctic also has a very high temperature variability at seasonal to interannual timescales, and the magnitude of warming is small compared to regional variability. Furthermore, as the Arctic warms, its temperatures become similar to temperature regimes elsewhere in the world. Thus, while rates of climate change in the Arctic are high, its thermal

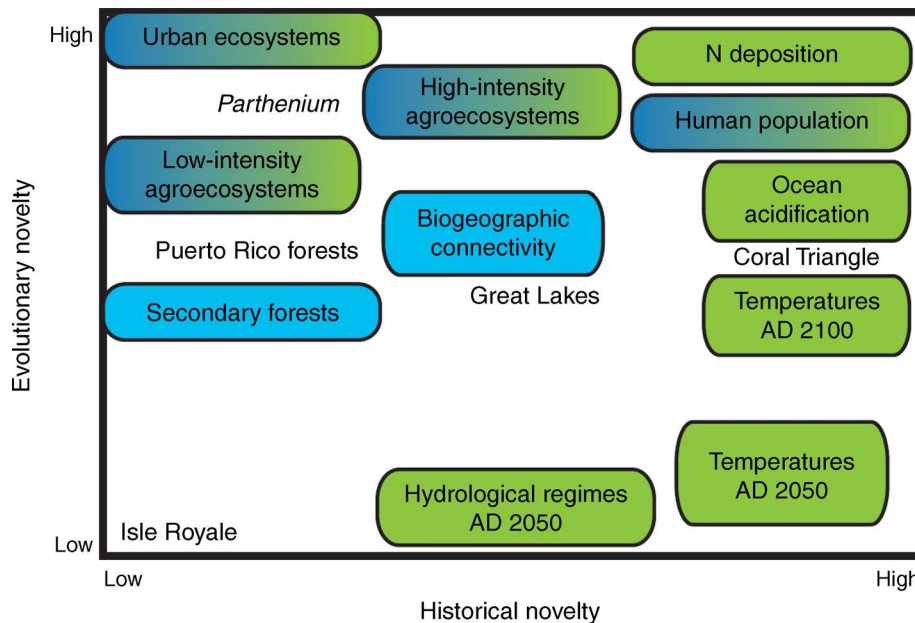


FIG. 1. Historical vs. evolutionary baselines. Some ecosystems or environmental conditions are highly novel with respect to the historical past (defined as the last several centuries), while others are unusual with respect to the evolutionary past (defined as the conditions present during the evolutionary lifetime of contemporary species). The historical time period is relevant because it is the primary basis for direct scientific observation and management experience, while the evolutionary baseline is relevant for assessing the adaptation capacity of species to, e.g., temperatures expected by AD 2100. For example, urban ecosystems are highly novel from an evolutionary perspective, leading to new emergent species interactions, while being relatively normal in the context of the last several centuries. Conversely, there are many geological analogs for projected temperatures by AD 2050, but this earth system state is outside direct societal experience. Some variables, e.g., current levels of human population and rates of atmospheric nitrogen deposition, have no precedent in either the historical or evolutionary past. The approximate position of our case studies relative to the two baselines is also shown (*Parthenium*, Puerto Rico forests, Isle Royal, Great Lakes, and Coral Triangle). See *The rise of novelty in ecosystems: Case studies*.

novelty may be low, at least at a global scale (Williams et al. 2007). In contrast, the absolute rates of temperature rises in the tropics are much smaller, but, as the tropics warm, they shift towards a state for which there is no recent precedent elsewhere on the planet, making climates there historically novel (Fig. 1; Williams et al. 2007, Mora et al. 2013, Garcia et al. 2014). Lack of novelty does not reduce concerns about the ecological effects of Arctic climate change, but does indicate that Arctic temperature changes may be less of a venture into the unknown than are tropical temperature rises.

When assessing novelty, the crucial question is: novel relative to what? The reference baseline has to be defined in both space and time. Spatially, it is crucial to define whether an ecosystem is highly novel relative to prior ecosystems in its particular location or to ecosystems in the same region, continent, or even globally. Temporally, one important baseline is the *historical* baseline (Fig. 1), for which the definition varies by place and culture, but which is often placed near a proposed start of the Anthropocene, ca. AD 1800 (Steffen et al. 2011). This baseline represents the recent environmental changes to ecosystems that are reasonably well characterized in the scientific literature, and have been managed in recent experience. A second relevant temporal baseline is the *evolutionary* baseline (Fig. 1),

i.e., the ecosystems that have existed over the last several million years. The evolutionary baseline represents the range of conditions that lineages leading to current species of higher orders have experienced, adapted to, and survived during their evolution (Bartlein and Prentice 1989). If novelty is high relative to the evolutionary baseline, then species are more likely to have limited adaptive capacity to these new conditions (Corlett 2012). Other baselines could be used, such as a baseline placed prior to the late Quaternary extinctions of megafauna and the ecological effects stemming from their losses (Gill et al. 2012, Doughty et al. 2013).

Why is novelty important and why is it important to measure? From a scientific perspective, highly novel ecosystems are paradoxical: they offer us new systems to study and opportunities to test ecological theories, while often reducing our confidence in future forecasts. From a management perspective, a challenge of novelty is that as the future looks less and less like the past, historical baselines become an increasingly tenuous management goal. This does not mean that historical baselines become irrelevant; indeed our definition of novelty emphasizes the need to assess change relative to a baseline. However, high abiotic novelty may make it increasingly difficult, for example, to maintain protected areas in their current state, or to restore ecosystems to a

historical baseline or trajectory (Harris et al. 2006, Hobbs et al. 2006; but see Murcia et al. 2014). Hence, conservation and restoration goals may have to be reassessed where novelty is high.

In summary, in our conceptualization, novelty is everywhere, but at varying degrees, it occurs in many abiotic and biotic dimensions, it can and should be quantified, and it is only meaningful to talk about levels of novelty relative to a specific temporal and spatial baseline. Over the last century, high novelty has primarily been due to biotic processes, e.g., the spread of nonnative species, and land use change. In the coming century, abiotic drivers such as climate are likely to be the main cause for rising novelty. In the following sections, we illustrate our conceptualization of novelty with a series of case studies, show how at least some dimensions of novelty can be quantified and mapped, then discuss the implications of rising novelty for the science of ecology and for conservation practice.

THE RISE OF NOVELTY IN ECOSYSTEMS: CASE STUDIES

To illustrate the themes and contrasts that we highlight as central to characterizing novelty, including the role of biotic vs. abiotic factors as causes of novelty, we describe five case studies of ecosystems where novelty is either already high or is expected to become so, where there are differences in historical vs. evolutionary novelty, and describe how unintentional and intentional human action has contributed to novelty in these ecosystems. We did not attempt to account for every aspect of change at every timescale, but rather focused on a dominant aspect of novelty to highlight the different ways in which novelty has occurred and will continue in the future. An overarching theme is the pervasiveness of the rise of novelty in these ecosystems, even in those carefully managed to preserve wildness.

Parthenium rangelands

Our first example is a highly novel rangeland ecosystem, where novelty is caused by the spread of a nonnative species. *Parthenium hysterophorus* (L.) (Fig. 2a) is a noxious forb (*Asteraceae*) native to the American tropics that has been widely dispersed since the 1950s (Fig. 2b) through food grains (including via food aid programs) and contaminated pasture seed (Kohli et al. 2006). The species is a major weed in rangelands in Australia and India, and of increasing concern in countries bordering India, and in eastern and southern Africa. Once introduced, *Parthenium* tends to dominate large areas because of its allelopathy (McFadyen 1992). One reason for the success and dominance of *Parthenium*, similar to many other nonnative plants, is its use of “novel weapons,” i.e., biochemicals that native species had never previously encountered (Callaway and Ridenour 2004).

Areas invaded by *Parthenium* provide substantially lower ecosystem services. Forage production can de-

crease up to 90% (Nath 1988), and *Parthenium* can cause allergic skin reactions, lesions in the mouth and intestines, and death of livestock foraging on invaded rangelands. Cattle grazing on even mildly infected areas produce milk and meat unfit for human consumption (Kohli et al. 2006).

Eradication of *Parthenium* and the restoration of invaded areas has proven to be challenging, and may only be feasible locally (Adkins and Shabbir 2014). Control with herbicides requires high concentrations, and *Parthenium* can regenerate from underground parts (Kohli et al. 2006). Hence, *Parthenium* rangelands are an example of an ecosystem, present today, that is highly novel in terms of its species composition and relative to an evolutionary baseline, given its mixture of formerly biogeographically separated species. *Parthenium* is also an example of novelty with substantial undesirable outcomes and where accepting the rise of novelty is tantamount to accepting the loss of biodiversity, and ecosystem services (Murcia et al. 2014, Wuerthner et al. 2014).

Puerto Rico

We next turn to an example in which the mixture of native and nonnative species has also produced highly novel species compositions relative to an evolutionary baseline, but these have potentially high conservation value. In the 1820s, pastures covered approximately 55% of the Caribbean island of Puerto Rico, by 1900 more than 75% of the island was deforested (Wadsworth 1950), and in the 1940s, forests covered only <10% of the island, with most of the coastal plains and mountain slopes used for sugarcane, pasture, coffee, and subsistence farming. Changes in the political status and economy of Puerto Rico in the late 1940–1950s resulted in large-scale agricultural abandonment (Rudel et al. 2000), followed by mostly unassisted growth of early-successional forests, especially in the central mountains. Forest cover increased to 30% in 1980, 41.6% in 1992, and to 50–57% in the early 2000s (Brandeis et al. 2007). Early stages of forest succession on former agricultural and pasture lands are heavily dominated by nonnative tree species (Lugo and Helmer 2004). The biotic novelty of these forests is high, with introduced species accounting for up to 60% of the importance value in dry post-agricultural forests of southwestern Puerto Rico (Fig. 2c). However, these forests are providing habitat for native forest bird species (Lugo et al. 2012), and these birds are contributing to the reestablishment of native trees through their role as seed dispersers (Martinez 2010).

The forests on the former sugarcane fields of Puerto Rico, like the *Parthenium* example, thus represent highly novel ecosystems from an evolutionary perspective. Key agents of novelty are the introduction of forest species and the legacies of past land use. However, unlike the *Parthenium* example, several benefits may accrue with the

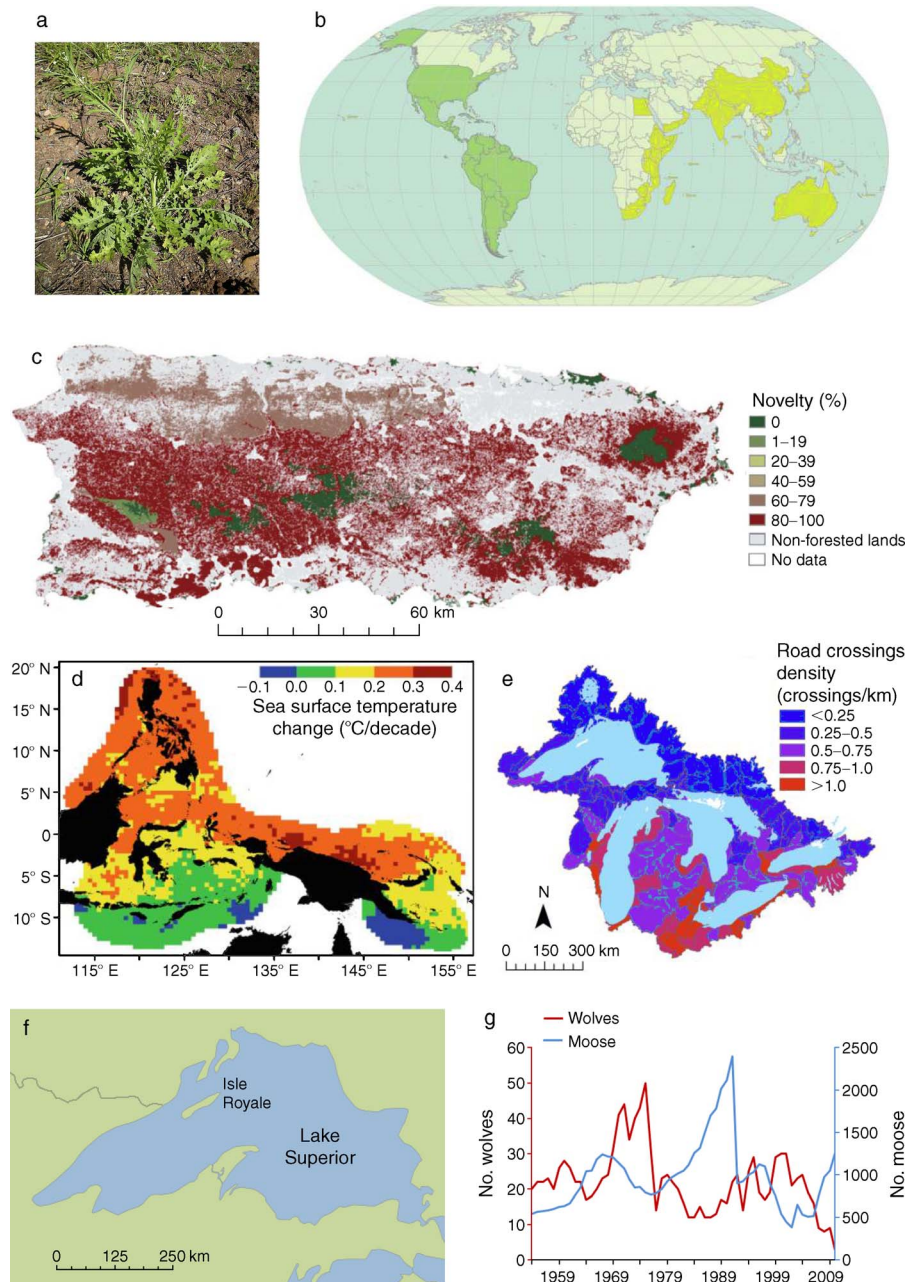


FIG. 2. Visuals related to our case studies including (a) *Parthenium hysterophorus*, (b) the native distribution of *Parthenium* in dark green, and its introduced distribution in light green (data courtesy of S. Adkins), (c) modeled levels of novelty in the forests of Puerto Rico based on the presence of introduced tree species in survey plots (adapted from Martinuzzi et al. 2013; in this study from Puerto Rico, novelty was modeled based on the percentage of trees in survey plots that were introduced species), (d) changes in sea surface temperature in the Coral Triangle from 1985 to 2006 (from Penafior et al. 2009), (e) density of road crossings for streams in the Great Lakes watershed (adapted from Januchowski-Hartley et al. 2013), (f) the location of Isle Royale in Lake Superior, and (g) the time series of wolves and moose on Isle Royale (data courtesy of J. Vucetich).

emergence of novelty here. Nonnative trees are restoring many of the ecosystem functions of the native forests that existed prior to deforestation. Scientifically, the Puerto Rico forests and similar tropical secondary forests offer opportunities to test theories about species coexistence and ecosystem function in the absence of deep co-

evolutionary relationships among many species pairs (Mascaro et al. 2011, Atkinson and Marin-Spiotta 2015). In this case, high biotic novelty may thus represent an opportunity for ecological science, species conservation, and restoration, highlighting that management response to novelty needs to be site specific and nuanced.

Coral Triangle

In our third case study, we focus on the Coral Triangle of the Indo-Pacific as an example of an ecosystem likely to be transformed by the rise of novelty in at least two key abiotic variables: seawater temperatures and pH (Fig. 2d). The Coral Triangle encompasses one-third of the world's coral reefs, and three quarters of all coral species (Burke et al. 2012). At the same time, the Triangle is home to 120 million people, many of whom depend on the reef ecosystems for food, income, and cultural services (Hoegh-Guldberg et al. 2007), but coastal development, pollution, and overfishing pose additional threats (Burke et al. 2012).

By 2050–2100, atmospheric temperatures and CO₂ concentrations will certainly be higher than at any other point within the past 800 000 years (Hoegh-Guldberg et al. 2007). Sea surface temperatures in the Coral Triangle are rising by 0.2°C per decade (Penaflor et al. 2009), and projected to increase by 1°–4°C by 2100. Increases of 2°C are likely to eliminate most reefs (Hoegh-Guldberg et al. 2009) because rising seawater temperatures cause coral bleaching. Indirect consequences of bleaching include a higher vulnerability of corals to disease and bioeroders (e.g., parrotfish), and loss of habitat for fish and other biota.

In addition to warming, ocean acidification threatens coral reef ecosystems. Between 2020 and 2050, seawater pH in the Coral Triangle is expected to decline to or fall below levels required for corals to maintain CaCO₃ reef structures (Hoegh-Guldberg et al. 2009). Even before that threshold is reached, ocean acidification will cause lower growth rates and coral densities, increased exposure to eroder fishes, reduced structural complexity, reduced habitat quality and diversity, and reduced reproductive success of coral. Unfortunately, adaptation of corals to temperature increases and acidification is unlikely to match the high rates of change in pH and temperature.

In summary, abiotic conditions in the Coral Triangle may not yet be highly novel, but have already changed substantially (Penaflor et al. 2009), and these changes are expected to continue through 2100, resulting in high abiotic novelty relative to conditions within the past 800 000 years (Hoegh-Guldberg et al. 2007). These changes in abiotic conditions are essentially uncontrollable by local resource managers. The future of the Coral Triangle in the face of high abiotic novelty is highly uncertain, and the potential for surprises and unintended consequences of management actions is high.

Great Lakes

The North American Great Lakes and their tributaries offer an example of a highly complex socio-ecological system in which high levels of novelty are at least partly intentional. Here, one major dimension of novelty is the diminished ecological connectivity of

stream networks due to the construction of hundreds of thousands of dams and road crossings (Fig. 2e).

The Great Lakes basin is the single largest freshwater ecosystem in the world, containing 21% of the world's surface freshwater, and home to 33.5 million people with high dependence on a variety of lake-derived ecosystem services. Prior to European settlement in the 19th century, large breeding migrations of native fishes extended far inland. Today, Great Lakes tributaries are fragmented by nearly 8000 dams and 268 000 road crossings (Januchowski-Hartley et al. 2013). These structures block critical movements of native fishes such as lake sturgeon (*Acipenser fulvescens*), and influence water temperature and the downstream flux of water, sediment, and nutrients (Ligon et al. 1995).

Many stream barriers were put in place intentionally to provide navigation, flood control, recreational services (Ligon et al. 1995), and nonnative species control (Lavis et al. 2003). Reservoirs can support economically important recreational fisheries, and recreational fishing hotspots when migratory fish congregate below them. Furthermore, dams can limit the runoff of agricultural sediments and nutrients into the Great Lakes.

Removing dams and improving culverts helps restore aquatic connectivity for native migratory species, but in some cases this may increase other aspects of novelty. While barriers cause high novelty in terms of reduced hydrological connectivity, they also stem the rise of novelty by restricting the spread of pathogens, such as viral hemorrhagic septicemia, and nonnative species, like sea lampreys (*Petromyzon marinus*). Sea lampreys were one of the main reasons for the collapse of lake trout populations, and the impact of sea lampreys would be worse if they were able to access the breeding habitat upstream of impassable dams and road crossings (Neeson et al. 2012).

The Great Lakes are a large and complex ecosystem, and the drivers and manifestation of novelty in the Great Lakes are similarly complex, arising from the interactions among altered hydrological, connectivity, species introductions, and the joint responses of native aquatic species to these changes. In the Great Lakes, with its high levels of intentional novelty in stream network connectivity (relative to historical baselines), management choices are thus far from obvious. Restoring prior landscape connectivity would likely have substantial unintended consequences, due to the spread of nonnative species and pathogens, and cause the loss of new ecosystem services. In the prior three examples, the rise in novelty was unintentional, and reversing novelty may be socially acceptable or even desirable, even if difficult to achieve in practice. In the Great Lakes ecosystem, much of the current novelty emerges directly from intentional alterations of ecosystems by humans, with the goal of providing specific ecosystem services, and reversing novelty would likely face strong opposition.

Isle Royale

Our last example highlights the pervasiveness of novelty and the vexing question that even low levels of novelty pose for science and conservation. In the middle of Lake Superior, the largest and northern-most of the Great Lakes in North America, lies Isle Royale (Fig. 2f). It is the least visited of all the National Parks in the conterminous United States, a place designated to let ecological processes run their course, and where the population dynamics of predators and prey, in this case wolves (*Canis lupus*) and moose (*Alces alces*), have been studied for over 60 years (Fig. 2g), shortly after wolves recolonized the island (Peterson et al. 1998). However, the wolf population is on the brink of extirpation, struggling against genetic bottlenecks, introduced pathogens transmitted by dogs, winters too warm to form an icebridge to allow wolves to migrate to the island, and development along the Canadian shore that makes such migration events less likely even if there was enough ice (Mlot 2013). This makes Isle Royale both a place as pristine as one can find today in the conterminous United States, and one that is fundamentally changed by nonnative pathogens, climate change, and intensifying land use on nearby shores. Again, management responses are far from clear. As the wolves are threatened by extirpation, what is the right conservation action? To let natural processes run their course and Isle Royale lose its wolves, or to assist their migration from the mainland with crates and boats? Given the scientific value of the long-term study on the cycles of predator and prey, which management actions would result in the greatest scientific understanding: to accept the loss of the top predator and monitor changes or to preserve the cycles of wolves and moose? There are no easy answers (Mlot 2013). Isle Royale is still very much a wild ecosystem, with very close similarities to historical counterparts, yet even Isle Royale is changing, along trajectories subtly different from historical precedents, making conservation decisions difficult.

Our case studies highlight the large range in the levels of novelty from fairly minor (Isle Royale) to very high (*Parthenium*, and Puerto Rico). High levels of novelty can result from either abiotic (Coral Triangle), or biotic change (*Parthenium*), or both (Great Lakes). Some places are already highly novel relative to both an evolutionary and a historic baseline (Puerto Rico), while others will become highly novel in the future (Coral Triangle). High levels of novelty can have negative effects on biodiversity and ecosystem function (*Parthenium*), even when novelty is intentional (Great Lakes), while other highly novel ecosystems offer conservation opportunities (Puerto Rico). At the same time, even low levels of novelty can present major conundrums for conservation (Isle Royale). Taken together, our case studies demonstrate the need for a conceptualization of novelty in ecosystems that captures the reality that novelty is present everywhere but at varying levels, that novelty is increasing in many places, that novelty is

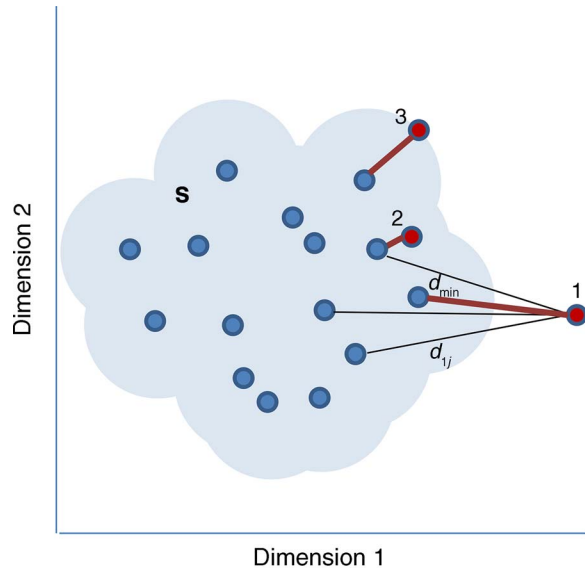


FIG. 3. Novelty can be quantified by calculating the distance (d_{ij}) between entity i and every member j of baseline set S for a set of abiotic or biotic variables of interest, e.g., winter minimum temperature, rates of nitrogen deposition, species richness, or the abundances of individual species. The degree of novelty is then defined as the minimum distance ($d_{i,min}$), i.e., the distance between i and its closest counterpart in set S . Entity i is defined to be “no-analog,” i.e., have no analog to any entity in set S , if $d_{i,min}$ is greater than a dissimilarity threshold defined by the analyst. In this example, blue dots indicate members of set S and red dots 1, 2, 3 indicate three entities for which their novelty relative to S is being evaluated. Thin black lines indicate the distances (d_{ij}) between entity 1 and selected members of entity S . Thick red lines indicate the minimum distance (d_{min}) for entities 1, 2, and 3 to their closest analogs in S . Entity 1 has no close analog anywhere in set S , and so receives a high novelty score (i.e., a high d_{min}). This example shows two variable dimensions (with the novelty of entity 1 attributable to the x -axis variable), but the approach can be extended to multiple variables using standard metrics of multivariate dissimilarity (Legendre and Legendre 1998).

multidimensional with the relevant variables varying among ecosystems, and that assessing novelty requires a temporal and spatial reference.

QUANTIFYING AND MAPPING LEVELS OF PRESENT AND FUTURE NOVELTY WORLDWIDE

Conceptualizing novelty as a continuous variable lends itself to quantitative assessments using metrics drawn from community ecology and paleoecology (Fig. 3). In the following, we present a global assessment of terrestrial, abiotic novelty, both for the present and for the projected future, to illustrate one approach to measuring novelty and to highlight both the spatial variability in levels of novelty and the rise of novelty from now to the future. We focus on novelty in abiotic factors plus human population, because these factors have been key determinants of the emergence of novelty in ecosystems (Jackson and Overpeck 2000, Williams and Jackson 2007). Moreover, abiotic novelty is

typically a factor that a conservationist or land manager cannot control. Thus high abiotic novelty presents a challenge different, for example, from high biotic novelty due to a nonnative species, which management actions may be able to limit.

In our global assessment, we quantified novelty based on three abiotic variables (temperature, precipitation, and atmospheric nitrogen deposition) plus human population. These variables have powerful direct and indirect effects on biodiversity and ecosystem function, have changed greatly over the last century, and are projected to continue to change. We assessed novelty only for terrestrial areas, not the oceans or inland waters. Our resulting maps of novelty based on abiotic factors and human populations do not necessarily imply patterns of biotic novelty, but rather an integrated set of factors likely to cause high biotic novelty, either in the present (due to historical changes) or the near future (due to projected changes). Others have made maps of climate novelty (Williams and Jackson 2007, Williams et al. 2007, Garcia et al. 2014). Our main new contributions here were to, first, create an index that combines abiotic and anthropogenic drivers of novelty and, second, compare patterns of novelty today relative to a historical baseline vs. those in the future relative to today.

We measured novelty relative to two temporal baselines: present novelty relative to a historical baseline and projected future novelty relative to the present. We obtained data for three time periods: historical (late 19th to early 20th century), present (late 20th to early 21st century), and future (mid 21st century). The spatial extent of our reference baseline is global, in order to identify globally novel configurations of climatic and anthropogenic drivers of ecosystem change. We measured novelty by calculating, for each 0.5° grid cell, its dissimilarity to all grid cells in the reference baseline (e.g., a single modern grid cell vs. all late-19th century grid cells) and retaining the minimum dissimilarity. Higher minimum dissimilarities indicate higher novelty relative to the baseline. The use of minimum dissimilarity scores to quantify novelty has become increasingly common in climate change science, with standardized Euclidean and Mahalanobis being the most popular distance metrics (Williams et al. 2007, Garcia et al. 2014). We first calculated the dissimilarities between all pairwise comparisons of historical vs. modern grid cells, and modern vs. projected grid cells, using the standardized Euclidean distance (SED)

$$\text{SED}_{ij} = \sqrt{\frac{\sum_{k=1}^n (b_{ki} - a_{ki})^2}{s_{kt}^2}}.$$

The index k refers to each of the indicator variables and defines the multivariate space; here $n = 4$ (temperature, precipitation, global population, and atmospheric nitrogen deposition). The term a_{kj} gives the value of variable k at grid cell a_j drawn from the baseline reference set, which

is the set of all historical grid cells for the assessment of present novelty, and the set of all modern grid cells for the assessment of future novelty. The term b_{kj} is the value of k for grid cell j , for which novelty is being assessed.

For the assessment of present novelty, all grid cells b_j are drawn from the modern data set, while for the assessment of future novelty, all grid cells b_j are drawn from the future projected data set. The s_{kt} are the standard deviation of k across all terrestrial grid cells (i.e., across space) for baseline time period t . Dividing each variable by its variance (s_{kt}^2) standardizes all variables to a common scale and effectively downweights variables with high spatial heterogeneity, i.e., differences between grid cells are considered important only if they are large relative to background heterogeneity.

Temporal variability is generally preferred for standardizing variables, because it scales differences relative to the temporal environmental heterogeneity experienced by organisms at a location (Williams et al. 2007), but interannual data were not available for the population and nitrogen data, which is why we relied on spatial variability for all variables for consistency. This definition of abiotic novelty resembles the concept of climate velocity (Loarie et al. 2009, Ordóñez et al. 2014) but represents a distinct axis of risk (Garcia et al. 2014): high velocities pose risks to species unable to keep up, while high novelty indicates regions of the world where rates of change have pushed environments and ecosystems beyond historical ranges of variation (Mora et al. 2013).

We measured both local change and global novelty. Local change is the SED calculated when $i = j$, i.e., the difference between future and baseline values of the same grid cell. Global novelty was quantified by the minimum SED (SED_{\min}) between future values of a grid cell and the global pool of grid cell at the baseline. A $\text{SED}_{\min} = 0$ indicates that a grid cell has an exact analog in the baseline data. Increasing values of SED_{\min} indicate more dissimilarity between a grid cell and its closest analog. Thus, higher values of SED_{\min} correspond to higher novelty.

We obtained historical climate data from the University of Delaware Center for Climatic Research; present climate data from the WorldClim data set (Hijmans et al. 2005); and future climate projections from an ensemble of 12 Earth system models for Representative Concentration Pathway 6.0. Atmospheric nitrogen deposition data were based on atmospheric transport models of historical, present, and future nitrogen deposition (Dentener 2006). Historical population data were from HYDE (Goldewijk et al. 2011), and projected populations (to AD 2025) were from the *Gridded Population of the World (available online)*¹² and the United Nations. We interpolated or resampled all data to a common resolution of 0.5° . Data sources are described in detail in the Appendix.

¹² <http://sedac.ciesin.columbia.edu/data/set/gpw-v3-population-count-future-estimates>

The global assessment identified large areas with high novelty due to abiotic factors and human populations relative to the past (Fig. 4a), as well as widespread future increases in novelty (Fig. 4b). Areas of high current novelty relative to historical conditions were concentrated in the eastern United States, central Europe, eastern Brazil, and parts of India, and China. Arctic regions and northern Australia were secondary regions of high novelty. The present distribution of areas of high novelty was strongly influenced by human population growth and rising atmospheric nitrogen deposition; climatic changes had relatively small effects (Fig. 4c). In the future, novelty relative to today will be particularly high in East Africa, the Arabian Peninsula, India, China, and Australia. In North America and Europe, areas where novelty is already high will become even more novel in the future. Future novelty in the Arctic was projected to increase relative to current novelty, primarily due to changes in precipitation. Projected rates of temperature rise are large for the Arctic with major implications for the structure and functioning of Arctic ecosystems, but these future Arctic temperatures have analogs elsewhere in the climate system today (Williams and Jackson 2007). In contrast, high future novelty in the tropics and subtropics is due to temperature increases beyond the current global range of temperature. Overall, temperature and nitrogen deposition were the most important causes of future novelty (Fig. 4d).

Our approach to quantifying novelty has some limitations and our maps are intended to be illustrative, rather than definitive, global-scale maps of levels of current and future novelty. The most obvious limitation is that not all ways in which environments and ecosystems have been transformed can be easily quantified, either because variables cannot be easily measured now or were not measured during the historical baseline or both. Our maps provide one view of the global patterns of novelty in which novelty accrues linearly, critical thresholds are not accounted for, and the dimensions of novelty are additive and equally weighted. Novelty analyses based on different assumptions or other sets of variables likely would result in different spatial distributions of novelty. For example, novelty analyses based on seasonal temperature and precipitation data tend to highlight the tropics as the area of greatest future novelty (Williams et al. 2007, Garcia et al. 2014), while some ecosystem models predict a rise of novelty in ecosystems in the upper northern latitudes due to the shifting intersection of rising temperatures and stable insolation regimes (Reu et al. 2014).

Our assessment makes several important contributions. We advance prior work by moving beyond climate-only analyses to quantify multiple dimensions of novelty. Our analysis suggests that contributions of climatic variables to contemporary novelty are small relative to other anthropogenic variables, particularly

for the present (Fig. 4c). We also suggest that areas with a high human footprint (Sanderson et al. 2002) are also those where novelty is high relative to historical baselines. Our maps reinforce the point that novelty is globally pervasive and varying only in degree. They highlight major areas of novelty over the last century and those expected for the next 50 years. More generally, our approach provides a quantitative framework that can be extended to map novelty in other abiotic and biotic components of ecosystems depending on which variable set is most appropriate for a given scientific question or conservation challenge.

Implications of novelty for the science of ecology

Much of the debate among ecologists about novel ecosystems and the Anthropocene center on questions of conservation practice (Murcia et al. 2014, Wuerthner et al. 2014, Corlett 2015), which we return to in the next section. Here we ask instead the question: what can we learn from this emerging new world in which we ecologists find ourselves? From a scientific perspective, novel conditions pose a great opportunity and a profound challenge. On the side of opportunity, science is the study of the unknown, and highly novel ecosystems represent new frontiers of knowledge, offer new systems for study, and hence create opportunities to test ecological theories and develop new ones. On the other side, the behavior of highly novel ecosystems can be difficult to predict: abiotic novelty and resulting biotic novelty can result in new forms of population and species dynamics, new interactions among species, new rates of ecosystem processes, and potentially new stable states. Given this, it can be difficult to forecast the behavior of highly novel ecosystems of which we have little practical experience and for which there are only limited empirical observations (Williams and Jackson 2007, Williams et al. 2013). Providing ecological forecasts with a high information content and well-constrained uncertainties is a fundamental societal service of the ecological sciences (Clark et al. 2001), and the ability of ecology to deliver this service is challenged by an increasingly novel world.

However, while novelty poses a challenge for ecology, the ecological sciences have already embraced the study of novelty. The scientific literature is replete with studies of the responses of ecological systems to novel conditions: examples include the effects of elevated atmospheric nitrogen on biodiversity and ecosystem function (Dise and Wright 1995, Bobbink et al. 2010), comparisons of native and nonnative species (Sax et al. 2005), the effects of elevated CO₂ on plant physiology (Ainsworth and Long 2004), and responses of species to climates with no modern analog (Jackson and Overpeck 2000, Williams et al. 2001, Urban et al. 2012). Indeed, many core ecological concepts come from, or were strongly reinforced by, earlier studies of highly novel ecosystems. Examples include the principles of old-field succession (Cramer et al. 2008) and the trophic cascades

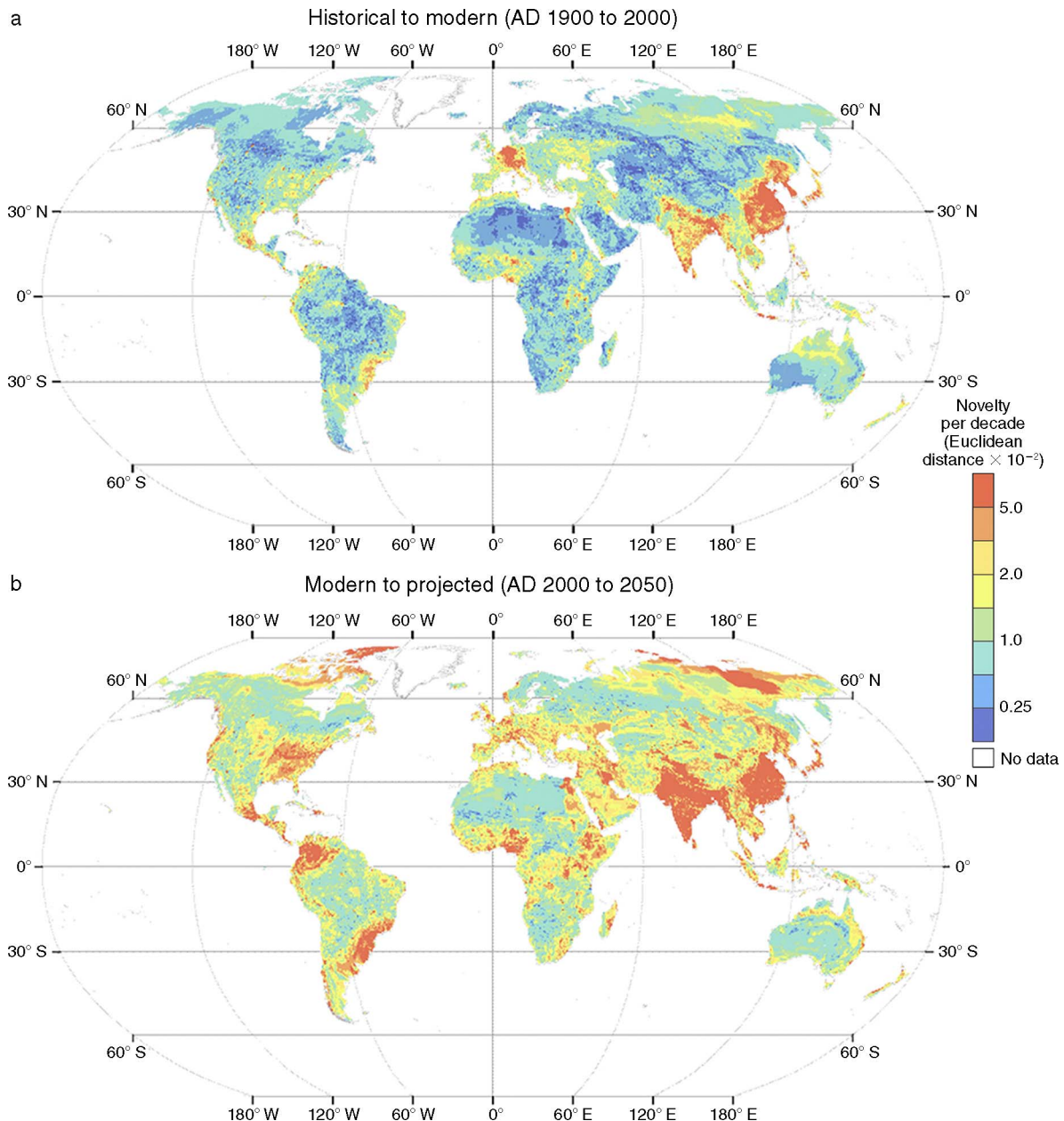


FIG. 4. Global assessment of novelty in several dimensions of the abiotic terrestrial environment (a) at present relative to the early 20th century, and (b) in the mid-21st-century relative to the present. The relative contribution of each of the four variables used to measure novelty is shown (c) at present relative to the early 20th century, and (d) in the mid-21st-century conditions relative to the present. Mapped values in (a) and (b) are minimum-dissimilarity scores, combined across annual temperature, precipitation, atmospheric nitrogen deposition, and human population density. High dissimilarities indicate that a grid cell lacks close analogs in the global set of terrestrial grid cells from the reference time period and thus that the environmental conditions there are highly novel. Low minimum dissimilarities do not necessarily indicate no change, but rather that some close analog exists for that grid cell in the reference time period, resulting in low novelty. Fig. 4 continues on facing page.

caused by the introduction of nonnative species or loss of apex predators (Estes et al. 2011). Ecology, as a discipline, has benefited from the study of novelty in ecological systems, and will continue to do so.

Abiotic and biotic novelty is now a global phenomenon, regardless of whether described based on the

indices of novelty that we used here (Fig. 4), distributions of anthromes (Ellis and Ramankutty 2008), human footprint (Sanderson et al. 2002), or novel climates (Williams et al. 2007, Mora et al. 2013, Garcia et al. 2014). Novelty offers an umbrella concept to conceptually link the many changes making ecosystems

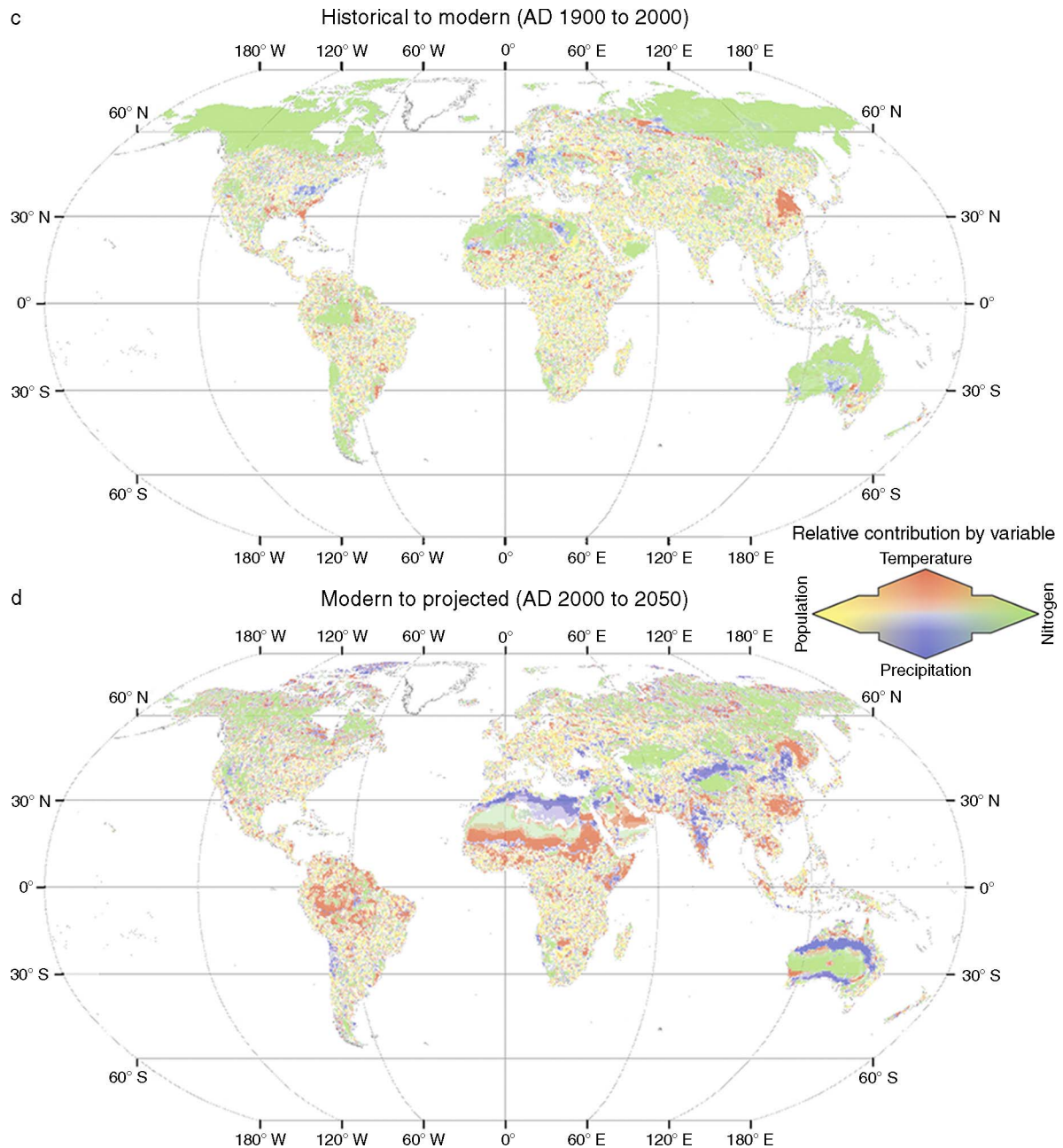


FIG. 4. Continued.

uniquely different from the past. The concept helps push ecology away from its traditional grounding in steady-state assumptions and toward a recognition that we are pursuing our science in a rapidly changing world, one that is already quite different from the recent past, and likely to become even more novel in the future. Approaches such as the multivariate indices that we demonstrated above offer tools to quantify the degree to which abiotic and biotic novelty occurs in different places. One key research question is to identify which metrics provide the most meaningful indices of novelty.

A second is to better understand the relationship between abiotic and biotic novelty, that is, to assess where biotic novelty has increased the most in response to which abiotic factors. And third, it is unknown how rising novelty is related to other global ecological trends such as biotic homogenization (McKinney and Lockwood 1999, Olden 2006, Martinez 2010). At one level, rising novelty and homogenization are related: the mixing of species lowers spatial heterogeneity in species composition and genetic structure (homogenization) while also creating species assemblages that differ

strongly from historic assemblages (novelty). However, new communities could also be highly homogenized, but have a historic precedent, resulting in low novelty. We do suspect that in most cases homogenization and novelty will co-occur, but this needs further study.

Novelty in ecosystems provides an impetus and an opportunity to reexamine existing theories and conceptual frameworks and extend them to accommodate the new world around us. For example, some theories of community stability invoke mechanisms based on coevolved relationships among species (Northfield and Ives 2013). If this is true, then highly novel ecosystems should be inherently less stable than historical ecosystems. Aside from the challenge of defining stability, this is a testable hypothesis, and one that could shed new insights into community stability theories. More broadly, can novelty rise to levels where major concepts in ecology no longer hold? Or are highly novel ecosystems merely new manifestations of well-understood processes?

Studies of highly novel ecosystems have already caused reexamination of the validity of some ecological concepts, while strengthening others. For example, on some islands, total species richness has increased, despite extirpations of native species, when the number of introduced species was higher than number of extirpations (Sax et al. 2002). Does this mean that species richness for these islands is essentially an unbounded quantity, with no saturation point, or with one that is very high (Sax and Gaines 2008)? Or is there an extinction debt still to be paid (Tilman et al. 1994), and if so, how widely do timelines to extinction differ among taxonomic groups?

Similarly, productivity–diversity theory predicts that the removal of species and losses of biodiversity degrades ecosystem functions such as primary productivity (Tilman et al. 2001). This raises the question of whether the opposite is true as well, i.e., if the addition of nonnative plant species, and an overall increase in plant richness, enhance certain ecosystem functions? Intriguingly, some highly novel forests characterized by a mixture of native and nonnative species in Puerto Rico and Hawaii exhibit higher or equivalent levels of above- and belowground biomass, productivity, and nutrient turnover than less-novel forests dominated by native species (Lugo and Helmer 2004, Mascaro et al. 2011). These results lend support to the productivity–diversity hypothesis while extending it to highly novel ecosystems in which the dominant phenomenon is the net addition, rather than net loss, of species.

High levels of novelty have already offered rich lines of inquiry for ecology. For example, urban ecosystems have become major loci of ecological research (Grimm et al. 2008) as have post-agricultural forests in New England (Foster et al. 2003) and the tropics (Atkinson and Marin-Spiotta 2015). The recognition that future climates may lack modern analogs has raised the

question of realized vs. fundamental niches and whether organisms living near the current thermal maximum of global climates have fundamental niches that extend beyond this maximum (Deutsch et al. 2008, Feeley and Silman 2010). Furthermore, climate-analog and climate-velocity analyses have identified where the speed and direction of climate change may trigger highly novel species mixtures (Webb 1986, Williams et al. 2001, Burrows et al. 2011). Community ecology shows how interspecific differences in competitive and dispersal ability can result in no-analog communities (Urban et al. 2012).

Although novelty in ecosystems provides new opportunities for scientific discovery, it also challenges our ability to forecast the future, especially when no-analog conditions occur. The “no-analog problem” is particularly thorny for species distribution modeling (Fitzpatrick and Hargrove 2009) if empirical species–climate relationships based on modern observations are used to forecast the effects of future climate change on species distributions and diversity (Elith and Leathwick 2009). For example, estimates of climate-driven biotic attrition in the tropics are highly sensitive to assumptions about whether species fundamental niches extend beyond the current range of climates (Feeley and Silman 2010), the narrowness of thermal niches for tropical species, and the dispersal capacity of organisms (Buckley et al. 2013). The recognition of future novelty and of the no-analog problem is pushing the ecological sciences forward in new directions. One is to advance the development of mechanistic models that directly represent ecological processes and thereby better predict ecological dynamics for system states outside the range of what can currently be observed (Kearney and Porter 2009). Species distribution models are increasingly being combined with other, more process-based ecological models, such as more sophisticated models of species dispersal, population demography, and population genetics (Franklin 2010, Fordham et al. 2014). Other approaches to tackling novelty include the study of species invasions and introductions to understand how species adapt to environmental conditions outside their native range (Early and Sax 2014), the use of the geological record to study biological dynamics during past periods of rapid and novel climates (Williams et al. 2013), and experimental manipulations designed to replicate key aspects of future no-analog environments such as higher-than-present CO₂, temperatures, and rates of nitrogen deposition (Ainsworth and Long 2004). Increasingly, these diverse modeling, experimental, observation, and paleohistorical lines of evidence are being integrated together to build a comprehensive understanding of biological dynamics during periods of rapid change and rising novelty (Dawson et al. 2011, Schimel et al. 2013), but much remains to be done.

A more pessimistic view is that the behavior of highly novel ecosystems may be fundamentally unpredictable

due to irreducibility, i.e., when a complex system cannot be predicted by a simplified model (Beckage et al. 2011). Key modeling challenges include specifying the niche characteristics of species under novel climates (Feeley and Silman 2010), predicting the effects of new species interactions (Blois et al. 2013), and parameterizing the ability of organisms to modify their environment and thereby construct their niches, moving into the “adjacent possible” (Beckage et al. 2011). However, absolute thermal limits have only been measured for a few taxa (Deutsch et al. 2008), and for most species, the effects of higher-than-present temperatures remain unknown. In this perspective, maybe the only certainty is that the future will be quite different from the present where novelty is high.

In summary, from a scientific perspective, the implications of highly novel ecosystems are paradoxical. On one hand, the prospect of future novelty (Fig. 4b) reduces the ability to confidently forecast future ecological dynamics, and inform environmental policy and management decisions. On the other hand, areas that are already highly novel (Fig. 4a) offer new opportunities to refine theory, collect observations, and improve our forecasting ability. In a similar vein, it is possible as a scientist to both be deeply concerned by current trends such as rising extinction rates and changing climates, yet be utterly fascinated by the opportunity to study systems undergoing rapid changes and moving into new states.

Implications of novelty for biodiversity conservation

Rapid rates of change all over the planet are often the impetus to conserve, protect, and restore ecosystems, and great strides have been made in safeguarding species (Pimm et al. 2014), creating protected areas (Radeloff et al. 2013), and restoring ecosystems (Cottam and Wilson 1966). Novelty presents challenges for conservation, however, that are different from those that change alone poses. Indeed, much of the debate about novel ecosystems has focused on the implications for conservation (Kareiva et al. 2011, Wuerthner et al. 2014) and restoration ecology (Hobbs et al. 2009, 2013, Moreno-Mateos 2013, Murcia et al. 2014) with sometimes heated differences in opinion (Woodworth 2013).

One proposed conservation approach is to protect areas where novelty is low and restore those where novelty is high (Woodworth 2013, Wuerthner et al. 2014). This approach certainly has merit, but protecting areas of low novelty alone will not suffice. Because of the continuum and pervasiveness of novelty, biodiversity conservation too must employ a range of approaches. Conservation cannot afford to give up on places where novelty is high, and ignore when such places offer conservation opportunities (Lugo 2012). Many approaches are already in the toolbox of conservation biologists and remain essential, including the establishment and maintenance of protected areas, species

reintroductions, incentives for sustainable management of working landscapes, regulation to limit harm to species and habitats, and education. However, conservation will have to change in the face of novelty and the concomitant challenges of managing and predicting the behavior of ecosystems increasingly diverging from historical baselines. Examples of such changes include (1) managing species and ecosystems for adaptation to a changing world, (2) developing adaptable conservation regulations and policies, and (3) becoming more explicitly experimental in conservation efforts. We discuss these examples in more detail in the following subsections.

Managing for adaptation

Species can adapt morphologically, physiologically, and behaviorally to environmental change and all species present today have adapted to past environmental change. Threatened species may be able to adapt behaviorally to highly novel ecosystems, and such behavioral adaptation should be fostered. An excellent example is the managed introduction of threatened Peregrine Falcons (*Falco peregrinus*) into urban environments (Tordoff and Redig 2001). There is hardly an environment more novel than the downtown urban areas where Peregrines now chase Rock Pigeons (*Columba livia*), a nonnative species. Peregrines' use of castles in Europe sparked the idea that other human constructions may be suitable habitat for them, and the introductions of peregrine falcons into cities were successful because cities are similar in habitat structure to Peregrines' natural habitat and provide abundant food resources. There may be many more opportunities where the recovery and survival of threatened species could be facilitated in highly novel ecosystems (Rodriguez 2006), especially when threatened species have high behavioral plasticity.

Related to this is the suggestion that protected area networks should be designed to be Noah's Ark, not Noah's Vault. That is to say that the ultimate goal should be for species to leave the ark at some point, and that protected areas should safeguard species for a while, not be forever their only refuge. In terrestrial conservation planning, generally little attention is given to how to design protected area networks in order to maximize the benefits to highly novel ecosystems in which they may be embedded. Instead, the focus is to maintain populations *within* protected areas, and to improve connectivity among them. When the surroundings of protected areas are taken into account, it is typically in terms of the threats posed to the protected areas (Hansen and DeFries 2007, Radeloff et al. 2010). As novelty rises, it becomes even more important to identify opportunities for species to adapt to adjacent habitats and to make this an explicit part of conservation planning (Knight and Landres 1998).

Adaptable conservation regulations and policies

Much of the regulatory framework for conservation is based on the assumption that ecological conditions are static, or that habitat can return to a prior stage after a disturbance ends or threat is abated. Where novelty is high, this may not be the case, and that may require laws, regulations, and management plans that are inherently adaptable without weakening the essential protections that they provide (Ruhl 2008, Craig 2010).

For instance, the Endangered Species Act (ESA) is one of the most powerful biodiversity conservation laws in the United States because it prohibits take (i.e., the killing, capture, or harm) of threatened and endangered species. However, a federal agency can issue a long-term permit that allows take if there is an approved plan for mitigation activities (Bernazzani et al. 2012). A “no surprises” policy assures landowners that no additional mitigation will be required even if unforeseen circumstances arise. Highly novel ecosystems make it quite likely that unforeseen circumstances will occur, making the ESA less effective. However, making the act more adaptable entails a strong risk that this would open the door to its weakening. The challenge is how to design regulatory frameworks that provide both strong protection and the ability to adapt to the unexpected surprises associated with rising novelty.

Unfortunately, recent trends in conservation policy may make it harder to adapt to high levels of novelty. One of these trends is the switch from land protection via outright purchase of land to the purchase of conservation easements on private lands that restrict future development and other land uses (Rissman et al. 2015). Conservation easements are popular for good reasons: purchasing only some of the rights is cheaper, and creates conservation opportunities when landowners are unwilling to sell their land but agreeable to easement restriction on their land use. The drawback is that perpetual easements inherently assume no change by fixing certain purposes, rights, and restrictions in perpetuity, often without identifying processes for changing these terms (Rissman et al. 2015). Furthermore, conservation easements confer only partial property rights, so land management agencies have much less discretionary authority on how to manage the land (Rissman et al. 2015). Hence, the lack of flexibility and the lack of discretionary authority may make current easements ineffective where novelty is high.

Appropriately nested governance is critical for building regulatory and policy frameworks that can accommodate novelty (Dietz et al. 2003). Federal regulation can be a powerful safeguard against conservation threats, but federal laws are most straightforward when aimed at easy targets, such as point-source pollution, and many of the easy targets have been reached. Moreover, federal regulations are difficult to customize

to local conditions, and can be slow to change as novelty rises. Local governance is typically much more adaptive, flexible, and iterative, and community-based efforts can provide critical knowledge and support to achieve behavioral change and conservation outcomes. However, relying only on local governance and communities will inevitably produce an uneven distribution of conservation efforts, and may not suffice when outside economic interests are strong. This is why nested governance is important, and there is a need to synchronize the scales of governance and rising novelty to learn and adapt in a timely fashion (Cash and Moser 2000).

Long-term adaptive management and experimentation

Given difficulties to predict the trajectories of highly novel ecosystems and appropriate management responses, there is a critical need for more experiments to test management actions, monitor their effects, and learn from natural experiments (NRC 2013). Adaptive management provides strong precedent (Walters and Holling 1990), but more needs to be done. In particular, given that climate change and its effects will take decades to unfold, there needs to be a commitment to long-term experiments with alternative management strategies, and thorough monitoring.

One example is to adopt an explicitly experimental approach to the management of protected areas and the matrix surrounding protected areas. We see a continued need to limit changes in some protected areas, especially those that harbor endemic species at risk of extinction with no viable relocation options, or ecosystems that are not found anywhere else (Prendergast et al. 1993). However, resources are lacking to limit change everywhere. One experimental design would be to vary approaches among and within protected areas, so that some protected areas are heavily managed to maintain the status quo, whereas others are not managed at all and other receive experimental management treatments to facilitate the transition of ecosystems along desired trajectories. Which areas would receive which treatment should be based upon current and future gradients in novelty.

Similarly, it is difficult to predict which species can persist in areas where abiotic novelty is high, and where changes may make current ranges unsuitable for many populations and species (Schwartz et al. 2012). This means that judicious experiments with assisted migration may be necessary to assess which species may be able to occupy highly novel ecosystems. Experiments with assisted migration, also referred to as managed relocation or assisted colonization, pose risks, including those that are associated with the introduction of nonnative species. However, fragmented landscapes ironically may provide an opportunity for experiments regarding assisted migration, because fragmentation can limit the potential spread of relocated species, making experimentation less risky.

CONCLUSIONS

We have no time for short-cuts

—German mountaineering proverb

The study of novelty in ecosystems represents ecology's grappling with the concept and implications of the Anthropocene, i.e., the recognition that humans have altered the world so much that humanity's collective activities may be now on the scale of geological forces (Marsh 1874, Steffen et al. 2011). Novelty, already high in many places, is likely to rise even further over the next hundred years. Our novelty now will be history for ecologists of the future; much of what seems new and strange now will become commonplace.

Measuring novelty, making the best forecasts possible of future environments and ecosystems, and identifying appropriate management responses for different levels and types of novelty will be major challenges for applied ecology and conservation for decades to come. Meeting this challenge will require advances in the science of ecology, creative new management and regulatory approaches, and critical reflection on the ethical implications of novelty (Callicott 2002, Minter and Collins 2010) that can provide "guidance for meeting ecological situations so new or intricate ... that the path of social expediency is not discernable to the average individual" (Leopold 1949).

Ecology and conservation find themselves in an increasingly novel world. This can be deeply unsettling, and abiotic and biotic novelty challenges both the science of ecology and the practice of conservation at its core. As scientists, rising abiotic and biotic novelty offers new systems to study, systems that are on trajectories where they have no analog in the recent past, or even in deeper evolutionary history. As conservationists, we have to redouble our efforts to protect the last great places, while realizing that such protection alone will not suffice, and that we must be creative about conservation approaches along the entire continuum of novelty. Neither cities nor protected wildlands, nor any of the places in between, can be sustained if the whole landscape in which they are embedded is not sustainable (Meine 2014). The rise of novelty is one of the great overarching challenges and opportunities for our generation of ecologists and conservationists. Simply ignoring novelty and wishing it was not there is not a solution, nor is the indiscriminate embrace of novelty, as tempting as both of these short-cuts may be.

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LITERATURE CITED

- Adkins, S., and A. Shabbir. 2014. Biology, ecology and management of the invasive parthenium weed (*Parthenium hysterophorus* L.). *Pest Management Science* 70:1023–1029.
- Ainsworth, E. A., and S. P. Long. 2004. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytical review of the responses of photosynthesis, canopy properties, and plant production to rising CO₂. *New Phytologist* 165:351–372.
- Atkinson, E. E., and E. Marin-Spiotta. 2015. Land use legacy effects on structure and composition of subtropical dry forests in St. Croix, US Virgin Islands. *Forest Ecology and Management* 335:270–280.
- Bartlein, P. J., and I. C. Prentice. 1989. Orbital variations, climate and paleoecology. *Trends in Ecology and Evolution* 4:195–199.
- Beckage, B., L. J. Gross, and S. Kauffman. 2011. The limits to prediction in ecological systems. *Ecosphere* 2:1–12.
- Bernazzani, P., B. A. Bradley, and J. J. Opperman. 2012. Integrating climate change into habitat conservation plans under the U.S. Endangered Species Act. *Environmental management* 49:1103–1114.
- Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate change and the past, present, and future of biotic interactions. *Science* 341:499–504.
- Bobbink, R., et al. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* 20:30–59.
- Bogan, M. T., and D. A. Lytle. 2011. Severe drought drives novel community trajectories in desert stream pools. *Freshwater Biology* 56:2070–2081.
- Brandeis, T. J., E. H. Helmer, and S. N. Oswalt. 2007. The status of Puerto Rico's Forests, 2003. USDA Forest Service Southern Research Station, Knoxville, Tennessee, USA.
- Buckley, L. B., J. J. Tewksbury, and C. A. Deutsch. 2013. Can terrestrial ectotherms escape the heat of climate change by moving? *Proceedings of the Royal Society B* 280. <http://dx.doi.org/10.1098/rspb.2013.114>
- Burke, L., K. Reytar, M. Spalding, and A. Perry. 2012. Reefs at risk revisited in the Coral Triangle. World Resources Institute, Washington, D.C., USA.
- Burrows, M. T., et al. 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334:652–655.
- Callaway, R. M., and W. M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2:436–443.
- Callicott, J. B. 2002. From the balance of nature to the flux of nature: the land ethic in a time of change. Pages 91–105 in R. L. Knight and S. Riedel, editors. Aldo Leopold and the

- ecological conscience. Oxford University Press, New York, New York, USA.
- Cash, D. W., and S. C. Moser. 2000. Linking global and local scales: designing dynamic assessment and management processes. *Global Environmental Change—Human and Policy Dimensions* 10:109–120.
- Chapin, F. S., III, and A. M. Starfield. 1997. Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change* 35:449–461.
- Ciais, P., et al. 2013. Carbon and other biogeochemical cycles. Cambridge University Press, Cambridge, UK.
- Clark, J. S., et al. 2001. Ecological forecasts: an emerging imperative. *Science* 293:657–660.
- Corlett, R. T. 2012. Climate change in the tropics: the end of the world as we know it? *Biological Conservation* 151:22–25.
- Corlett, R. T. 2015. The Anthropocene concept in ecology and conservation. *Trends in Ecology & Evolution* 30:36–41.
- Correa-Metrio, A., M. B. Bush, K. R. Cabrera, S. Sully, M. Brenner, D. A. Hodell, J. Escobar, and T. Guilderson. 2012. Rapid climate change and no-analog vegetation in lowland Central America during the last 86,000 years. *Quaternary Science Reviews* 38:63–75.
- Cottam, G., and H. C. Wilson. 1966. Community dynamics on an artificial prairie. *Ecology* 47:88–96.
- Craig, R. K. 2010. “Stationarity is dead”—long live transformation: five principles for climate change adaptation law. *Harvard Environmental Law Review* 34:9–73.
- Cramer, V. A., R. J. Hobbs, and R. J. Standish. 2008. What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution* 23:104–112.
- Cronon, W. 1995. The trouble with wilderness, or, getting back to the wrong nature. Pages 69–90 in W. Cronon, editor. *Uncommon ground: rethinking the human place in nature*. W. W. Norton, New York, New York, USA.
- Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332:53–58.
- Dentener, F. J. 2006. Global maps of atmospheric nitrogen deposition, 1860, 1993, and 2050. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.
- Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA* 105:6668–6672.
- Dietz, T., E. Ostrom, and P. C. Stern. 2003. The struggle to govern the commons. *Science* 302:1907–1912.
- Dise, N. B., and R. F. Wright. 1995. Nitrogen leaching from European forests in relation to nitrogen deposition. *Forest Ecology and Management* 71:153–161.
- Doughty, C. E., A. Wolf, and Y. Madhi. 2013. The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nature Geoscience* 6:761–764.
- Early, R., and D. F. Sax. 2014. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Global Ecology and Biogeography* 23:1356–1365.
- Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology and Evolutionary Systematics* 40:677–697.
- Ellis, E. C., and N. Ramankutty. 2008. Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment* 6:439–447.
- Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. *Science* 333:301–306.
- Feeley, K. J., and M. R. Silman. 2010. Biotic attrition from tropical forests correcting for truncated temperature niches. *Global Change Biology* 16:1830–1836.
- Fitzpatrick, M. C., and W. W. Hargrove. 2009. The projection of species distribution models and the problem of non-analog climate. *Biodiversity and Conservation* 18:2255–2261.
- Fordham, D. A., B. W. Brook, C. Moritz, and D. Nogués-Bravo. 2014. Better forecasts of range dynamics using genetic data. *Trends in Ecology & Evolution* 29:436–443.
- Foster, D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. *BioScience* 53:77–88.
- Franklin, J. 2010. Moving beyond static species distribution models in support of conservation biology. *Diversity and Distributions* 16:321–330.
- Garcia, R. A., M. Cabeza, C. Rahbek, and M. B. Araújo. 2014. Multiple dimensions of climate change and their implications for biodiversity. *Science* 344. <http://dx.doi.org/10.1126/science.1247579>
- Gill, J. L., J. W. Williams, S. T. Jackson, J. P. Donnelly, and G. C. Schellinger. 2012. Climatic and megaherbivory controls on late-glacial vegetation dynamics: a new, high-resolution, multi-proxy record from Silver Lake, Ohio. *Quaternary Science Reviews* 34:66–80.
- Goldewijk, K. K., A. Beusen, G. van Dreht, and M. de Vos. 2011. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Global Ecology and Biogeography* 20:73–86.
- Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. G. Wu, X. M. Bai, and J. M. Briggs. 2008. Global change and the ecology of cities. *Science* 319:756–760.
- Hansen, A. J., and R. DeFries. 2007. Ecological mechanisms linking protected areas to surrounding lands. *Ecological Applications* 17:974–988.
- Harris, J. A., R. J. Hobbs, E. Higgs, and J. Aronson. 2006. Ecological restoration and global climate change. *Restoration Ecology* 14:170–176.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.
- Hobbs, R. J., et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15:1–7.
- Hobbs, R. J., E. S. Higgs, and C. Hall, editors. 2013. *Novel ecosystems: intervening in the new ecological world order*. Wiley-Blackwell, Hoboken, New Jersey, USA.
- Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution* 24:599–605.
- Hoegh-Guldberg, O., et al. 2009. The Coral Triangle and climate change: ecosystems, people and societies at risk. WWF Australia, Brisbane, Australia.
- Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
- Jackson, S. T., and J. T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26(Supplement):194–220.
- Januchowski-Hartley, S. R., P. B. McIntyre, M. Diebel, P. J. Doran, D. M. Infante, C. Joseph, and J. D. Allan. 2013. Restoring aquatic ecosystem connectivity requires expanding inventories of both dams and road crossings. *Frontiers in Ecology and the Environment* 11:211–217.
- Kareiva, P. M., M. Marvier, and R. Lalasz. 2011. Conservation in the Anthropocene. *Breakthrough Journal* 1:29–37.
- Kearney, M., and W. P. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species ranges. *Ecology Letters* 12:334–350.
- Knight, R. L., and P. B. Landres. 1998. Conservation across boundaries. Island Press, Washington, D.C., USA.
- Kohli, R. K., D. R. Batish, H. P. Singh, and K. S. Dogra. 2006. Status, invasiveness and environmental threats of three tropical American invasive weeds (*Parthenium hysterophorus*

- L., *Ageratum conyzoides* L., *Lantana camara* L.) in India. *Biological Invasions* 8:1501–1510.
- Kueffer, C. 2014. Ecological novelty: towards an interdisciplinary understanding of ecological change in the Anthropocene. Page 19–37 in H. M. Greschke and J. Tischler, editors. *Grounding global climate change. Contributions from the social and cultural sciences*. Springer Science+Business Media, Dordrecht, The Netherlands.
- Lavis, D. S., A. Hallett, E. M. Koon, and T. C. McAuley. 2003. History of and advances in barriers as an alternative method to suppress sea lampreys in the Great Lakes. *Journal of Great Lakes Research* 29:362–372.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Second edition. Elsevier, Amsterdam, The Netherlands.
- Leopold, A. 1949. *A Sand County almanac*. Oxford University Press, New York, USA.
- Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams. *BioScience* 45:183–192.
- Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. *Nature* 462:1052–1055.
- Lugo, A. E. 2009. The emerging era of novel tropical forests. *Biotropica* 41:589–591.
- Lugo, A. E. 2012. Conundrums, paradoxes, and surprises: a brave new world of biodiversity conservation. Pages 1–12 in T. Schlichter and L. Montes, editors. *Forests in development: a vital balance*. Springer Science+Business Media, Dordrecht, The Netherlands.
- Lugo, A. E. 2013. Novel tropical forests: Nature's response to global change. *Tropical Conservation Science* 6:325–337.
- Lugo, A. E., T. A. Carlo, and J. M. Wunderle. 2012. Natural mixing of species: novel plant–animal communities on Caribbean Islands. *Animal Conservation* 15:233–241.
- Lugo, A. E., and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190:145–161.
- Marsh, G. P. 1874. *The earth as modified by human action: a new edition of "Man and Nature."* Scribner, Armstrong & Co., New York, New York, USA.
- Martinez, O. J. A. 2010. Invasion by native tree species prevents biotic homogenization in novel forests of Puerto Rico. *Plant Ecology* 211:49–64.
- Martinuzzi, S., A. E. Lugo, T. J. Brandeis, E. H. Helmer. 2013. Case study: geographic distribution and level of novelty of Puerto Rican forests. Chapter 9 in R. J. Hobbs, E. Higgs, and C. Hall, editors. *Novel ecosystems: intervening in the new ecological world order*. Wiley-Blackwell, Oxford, UK.
- Mascaro, J., R. F. Hughes, and S. A. Schnitzer. 2011. Novel forests maintain ecosystem processes after the decline of native tree species. *Ecological Monographs* 82:221–228.
- McFadyen, R. C. 1992. Biological-control against *Parthenium* weed in Australia. *Crop Protection* 11:400–407.
- McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14:450–453.
- Meine, C. 2014. What's so new about the "New Conservation"? Pages 45–54 in G. Wuerthner, E. Crist, and T. Butler, editors. *Keeping the wild: against the domestication of Earth*. Foundation for Deep Ecology, San Francisco, California, USA and Island Press, Washington, D.C., USA.
- Minteer, B. A., and J. P. Collins. 2010. Move it or lose it? The ecological ethics of relocating species under climate change. *Ecological Applications* 20:1801–1804.
- Mlot, C. 2013. Are Isle Royale's wolves chasing extinction? *Science* 340:919–921.
- Mora, C., et al. 2013. The projected timing of climate departure from recent variability. *Nature* 502:183–187.
- Moreno-Mateos, D. 2013. Is embracing change our best bet? *Science* 341:458–459.
- Morse, N. B., P. A. Pellissier, E. N. Cianciola, R. L. Brereton, M. M. Sullivan, N. K. Shonka, T. B. Wheeler, and W. H. McDowell. 2014. Novel ecosystems in the Anthropocene: a revision of the novel ecosystem concept for pragmatic applications. *Ecology and Society* 19(2):12.
- Murcia, C., J. Aronson, G. H. Kattan, D. Moreno-Mateos, K. Dixon, and D. Simberloff. 2014. A critique of the "novel ecosystem" concept. *Trends in Ecology & Evolution* 29:548–553.
- Nath, R. 1988. *Parthenium hysterophorus* L.—a review. *Agricultural Reviews* 9:171–179.
- Neeson, T. M., M. J. Wiley, S. A. Adlerstein, and R. L. Riolo. 2012. How river network structure and habitat availability shape the spatial dynamics of larval sea lampreys. *Ecological Modelling* 226:62–70.
- Northfield, T. D., and A. R. Ives. 2013. Coevolution and the effects of climate change on interacting species. *PLoS Biology* 11:e1001685.
- NRC. 2013. *Abrupt impacts of climate change—anticipating surprises*. National Research Council, Washington, D.C., USA.
- Olden, J. D. 2006. Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography* 33:2027–2039.
- Ordóñez, A., S. Martinuzzi, V. C. Radeloff, and J. W. Williams. 2014. Combined speeds of climate and land-use change of the conterminous US until 2050. *Nature Climate Change* 4:811–816.
- Penafior, E. L., W. J. Skirving, A. E. Strong, S. F. Heron, and L. T. David. 2009. Sea-surface temperature and thermal stress in the Coral Triangle over the past two decades. *Coral Reefs* 28:841–850.
- Peterson, R. O., N. J. Thomas, J. M. Thurber, J. A. Vucetich, and T. A. Waite. 1998. Population limitation and the wolves of Isle Royale. *Journal of Mammalogy* 79:828–841.
- Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344:987.
- Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365:335–337.
- Radeloff, V. C., F. Beaudry, T. M. Brooks, V. Butsic, M. Dubinin, T. Kuemmerle, and A. M. Pidgeon. 2013. Hot moments for biodiversity conservation. *Conservation Letters* 6:58–65.
- Radeloff, V. C., S. I. Stewart, T. J. Hawbaker, U. Gimmi, A. M. Pidgeon, C. H. Flather, R. B. Hammer, and D. P. Helmers. 2010. Housing growth in and near United States protected areas limits their conservation value. *Proceedings of the National Academy of Sciences USA* 107:940–945.
- Reu, B., S. Zaehle, K. Bohn, R. Pavlick, S. Schmidtlein, J. W. Williams, and A. Kleidon. 2014. Future no-analogue vegetation produced by no-analogue combinations of temperature and insolation. *Global Ecology and Biogeography* 23:156–167.
- Rissman, A. R., J. Owley, M. R. Shaw, and B. H. Thompson. 2015. Adapting conservation easements to climate change. *Conservation Letters* 8:68–76.
- Rodriguez, L. F. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions* 8:927–939.
- Rudel, T. K., M. Perez-Lugo, and H. Zichal. 2000. When fields revert to forest: development and spontaneous reforestation in post-war Puerto Rico. *Professional Geographer* 52:386–397.
- Ruhl, J. B. 2008. Climate change and the endangered species act: building bridges to the no-analog future. *Boston University Law Review* 88:1–62.

- Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. *BioScience* 52:891–904.
- Sax, D. F., and S. D. Gaines. 2008. Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences USA* 105:11490–11497.
- Sax, D. F., S. D. Gaines, and J. H. Brown. 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *American Naturalist* 160:766–783.
- Sax, D. F., B. P. Kinlan, and K. F. Smith. 2005. A conceptual framework for comparing species assemblages in native and exotic habitats. *Oikos* 108:457–464.
- Schimel, D. S., G. P. Asner, and P. Moorcroft. 2013. Observing changing ecological diversity in the Anthropocene. *Frontiers in Ecology and the Environment* 11:129–137.
- Schwartz, M. W., et al. 2012. Managed relocation: Integrating the scientific, regulatory, and ethical challenges. *BioScience* 62:732–743.
- Simberloff, D., C. Murcia, and J. Aronson. 2015. “Novel ecosystems” are a Trojan horse for conservation. *Ensia*. <http://ensia.com/voices/novel-ecosystems-are-a-trojan-horse-for-conservation/>
- Steffen, W., J. Grinevald, P. Crutzen, and J. McNeill. 2011. The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical Physical and Engineering Sciences* 369:842–867.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowack. 1994. Habitat destruction and the extinction debt. *Nature* 371:65–66.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845.
- Tordoff, H. B., and P. T. Redig. 2001. Role of genetic background in the success of reintroduced Peregrine Falcons. *Conservation Biology* 15:528–532.
- United Nations Population Division. 1999. The world at six billion. United Nations, New York, New York, USA.
- Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: competition and dispersal differences create no-analog communities and cause extinctions during climate change. *Proceedings of the Royal Society B* 279:2072–2080.
- Wadsworth, F. H. 1950. Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. *Caribbean Forester* 11:38–56.
- Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* 71:2060–2068.
- Webb, T., III. 1986. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* 67:75–91.
- Williams, J. W., J. L. Blois, J. L. Gill, L. M. Gonzales, E. C. Grimm, A. Ordonez, B. Shuman, and S. D. Veloz. 2013. Model systems for a no-analog future: species associations and climates during the last deglaciation. *Climate Change and Species Interactions: Ways Forward* 1297:29–43.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.
- Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences USA* 104:5738–5742.
- Williams, J. W., B. N. Shuman, and T. Webb III. 2001. Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology* 82:3346–3362.
- Woodworth, P. 2013. *Our once and future planet*. University of Chicago Press, Chicago, Illinois, USA.
- Wuerthner, G., E. Crist, and T. Butler. 2014. *Keeping the wild: against the domestication of Earth*. Foundation for Deep Ecology, San Francisco, California, USA and Island Press, Washington, D.C., USA.

SUPPLEMENTAL MATERIAL

Ecological Archives

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