Chapter 5

ORIGINS OF THE NOVEL ECOSYSTEMS CONCEPT

Joseph Mascaro[1], James A. Harris[2], Lori Lach[3], Allen Thompson[4], Michael P. Perring[5], David M. Richardson[6] and Erle C. Ellis[7]

[1]Department of Global Ecology, Carnegie Institution for Science, Stanford, California, USA

[2]Environmental Science and Technology Department, Cranfield University, UK

[3]Ecosystem Restoration and Intervention Ecology (ERIE) Research Group, School of Plant Biology and the Centre for Integrative Bee Research, University of Western Australia, Australia

[4]School of History, Philosophy, and Religion, Oregon State University, USA

[5]Ecosystem Restoration and Intervention Ecology (ERIE) Research Group, School of Plant Biology, University of Western Australia, Australia

[6]Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, South Africa

[7]Geography & Environmental Systems, University of Maryland, USA

"In such ways *anthropogenic ecosystems* differ from those developed independently of man. But the essential formative processes . . . are the same."

Arthur G. Tansley, 1935

5.1 INTRODUCTION

Reading Tansley's (1935) opus, combatively titled 'The use and abuse of vegetational concepts and terms' nearly a century on, is illuminating in many ways. For one, the prose leaps off the page in a manner rarely seen in ecology journals today: he moves through emotional states no modern editor would allow, gleefully deconstructing the exactitude of his 'old friend' Fredrick Clements' proposition of a 'climatic climax', a single terminus of succession for a whole biome. He betrays his academic nature, variously accepting and rejecting terms that appear throughout the literature. He accepts 'climax' (within which he notably allows slow gradual change), coins the term 'ecosystem' (surely his greatest gift to the field), then roundly rejects the idea that ecosystems are a kind of 'complex organism', a phrase he finds too inexact to be useful. He italicizes profusely (evidenced in the opening quotation, for which the emphasis is original), an effort to convey final authority; like Clements, Tansley exhibits ecology's roots in botany, where taxonomy and strict classification reigned.

The lasting value of Tansley's paper comes not in his concluding litany of terminology (most of which is now altered or abandoned), but in his flashes of uncertainty about nature. He raises questions to which he does not know the answer: "Is man part of 'nature' or not?" He frames the quintessential debate in early 20th century ecology without making a ruling: "Many ecologists hold that all vegetation is always changing. It may be so: we do not know enough either to affirm or to deny so sweeping a statement." With statements like these, Tansley hints at an important insight: strict definitions of ecosystem types may never be tractable because there is too much spatiotemporal variation to categorize.

The organizing objective of this chapter was to categorically define a *novel ecosystem*. Doing so at the outset would imply that we were already convinced of their existence as something separate from other ecosystems, a notion upon which our read of Tansley has cast doubt. We therefore begin not by declaring what novel ecosystems are or are not (a task which we shall come to presently) but by reviewing the foundational principles that point to the existence and importance of novel ecosystems. From these, and a brief review of previous formulations of the concept, we hope the idea will emerge for the reader as it has for the authors. We ultimately step into synthesis, and present a new framework for the novel ecosystems concept.

## 5.2 FOUNDATIONS OF THE NOVEL ECOSYSTEMS CONCEPT

The novel ecosystem concept rests on three foundational principles, the first of which follows from Gleason (1926): "It may be said that every species of plant is a law unto itself, the distribution of which in space depends on its individual peculiarities of migration and environmental requirements." In Gleason's time, ecology was populated largely by naturalists and botanists with an instinctual urge to classify. It is remarkable that he was able to look at the same forests and grasslands as his predecessors and devise so different a hypothesis to explain them, one that was abjectly allergic to classification. Gleason viewed communities as whisperers of organization: the ephemeral overlapping of ranges combined with a faint alignment. Decades went by before the individualistic concept became more widely accepted, but Gleason did live to see it embraced by giants such as John Curtis and Robert

Whittaker. When ecology mourned Gleason in 1975, Robert McIntosh wrote for *Torrey* that "Gleason's then heretical idea is now widely recognized as part of the conventional wisdom in ecology" (McIntosh 1975). Yet controversy remained.

Had he lived another decade, Gleason would have received a gift reserved for all but a few theoreticians: irrefutable proof. In the form of sediment from North American lakes, the past was being steadily disrobed by palynological studies (Davis 1981, 1983; Pielou 1991; Delcourt 2002). These samples, which were largely from a period of glacial retreat at the close of the Wisconsinan 8,000 to 14,000 years ago, painted a clear picture: in times of environmental change, tree species move as individuals and not as part of discrete communities or organisms (Fig. 5.1). While students from Madison to Cornell can rattle off tree and shrub species that 'characterize' the beech-maple forest association today, students visiting the same habitat in a previous interglacial would find mesic forests of quite different composition. Such patterns inspired one paleoecologist contributing to this volume to call himself a 'radical Gleasonian' (Jackson 2006). From the tropics, Janzen (1985) concluded that the seduction of species *belonging* to communities was better thought of as species *fitting* into a habitat.

The individualistic concept provides the raw biological material from which the novel ecosystems concept is made. Because the flora and fauna move independently of one another in response to their environment, communities are constantly in flux at some temporal resolution. Without this property of the biosphere, novel ecosystems would not be possible. In some areas, such as those undergoing secondary succession, the fluctuations may be rapid and repeatable; in others, such as those undergoing changes in temperatures or carbon dioxide concentrations, the 'fluctuations' may be directional and permanent. Temperature drove tree species to move during glacial advances and retreats (Davis 1981), while CO_2 concentrations in the ocean caused shifts in foraminifera communities (Pagani et al. 1999). Where the ranges of species expanded or contracted (whatever the cause), communities were altered. Most recently, a massive increase in the rate of species introductions has unfolded: prior to human arrival, Hawaii lacked reptiles, amphibians, flightless mammals and ants, yet now it has all in abundance (Ziegler 2002).

The earlier examples highlight community changes caused both by biotic (i.e. range shifts) and abiotic
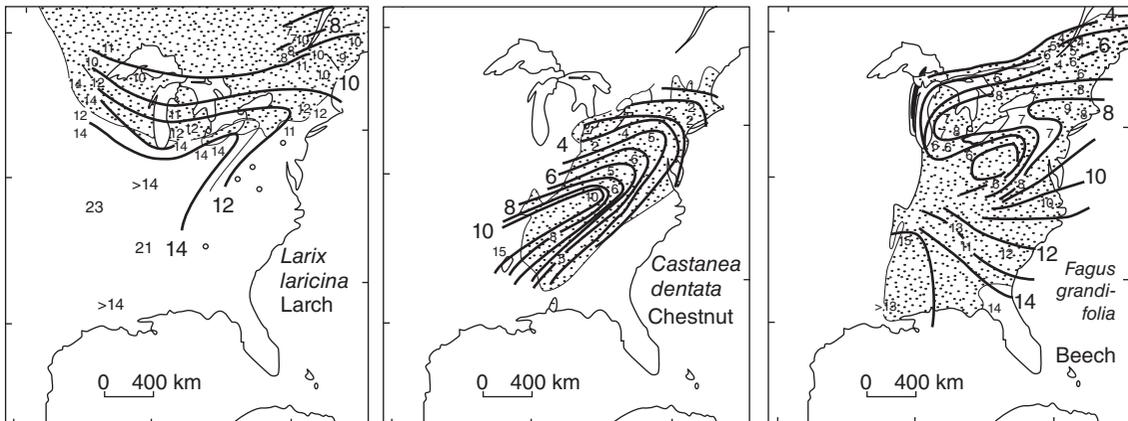
Figure 5.1 The Gleasonian framework of ecological communities. In the North American temperate forests shown, black bands indicate the southernmost extent for each species in time (1000 years). The varying trajectories of these ranges reflect the independent movement of each species as they coped with warming temperatures at the close of the Wisconsinan glaciation. From Davis (1983). Reproduced by permission of Missouri Botanical Garden Press.

forcing (i.e. responses to environmental change) and this leads to the second foundational concept upon which novel ecosystems rest: the biotic and abiotic characteristics of an ecosystem are tethered. They interact, following from one another and feeding back on one another (Tansley 1935; Jenny 1941; Odum 1969; Naeem 2002). Jenny (1980) made perhaps the most humorous declaration, calling the biotic factor ". . . a real bugbear. Like everybody else I could see that the vegetation affects the soil and the soil affects the vegetation, the very *circulus vitiosus* I was trying to avoid." Twenty years later, Naeem (2002) came to a similarly baffling (but editorially sanitized) conclusion: ". . . biodiversity is a product of its environment, and the antithesis, that the environment is, in part, a product of the organisms within it, is also correct." Empirical studies spanning the globe confirm strong interactions between the biotic and abiotic parts of ecosystems, from tubeworms mollifying habitat around oceanic vents (Cordes et al. 2003) to warming temperatures roasting tropical trees (Clark et al. 2003). Abiotic change leads to biotic change, and *vice versa* (this is, incidentally, why this book isn't called 'Novel Communities').

A third concept completes the groundwork for novel ecosystems: humans, like previously massive perturbations to the biosphere (Behrensmeyer et al. 1992; Vermeij 2005), cause changes in ecosystems that are directional and permanent. Indeed, Chapin and Starfield (1997) first invoked the term 'novel ecosystem' to characterize what they believed would be the ultimate outcome of anthropogenic changes to climate, disturbance regimes and species composition in boreal latitudes. Old views in terrestrial plant succession referred to human-modified ecosystems such as farms as "dis-climax" (Clements 1916). Note the root "dis" (having a negative or reversing force) and the similarity to the more modern term for the same systems: 'degraded' (reduced in rank). Humans have unequivocally had a negative impact on myriad species and ecosystems, particularly by co-opting land for the production of resources (Vitousek et al. 1997). However, when we are left to qualify a river that has increased in trophic complexity due to non-native fishes on Hawaii (Ziegler 2002), or an old Puerto Rican baseball field that is thick with pantropical tree species whose leaves have never before competed for sunlight (Lugo and Helmer 2004), we crumple at the term 'degraded'. To us, this term feels flawed and inexact. Clearly, neither 'degraded' nor its predecessor has sufficient descriptive power for ecosystems that are diverse and (in some cases) have undergone centuries of succession, or whose component species are experiencing unrestricted natural selection in their novel environs. Both terms imply change in a negative direction than can only be corrected by change in a positive direction,

when in fact *novel ecosystems* exist as a non-regressive consequence of human activity. They are simply not going back.

The widening recognition of pervasive anthropogenic change in ecosystems was the impetus for formalizing the novel ecosystems framework. Following a workshop in Granada, 2002, Milton (2003) reported that an 'emerging ecosystem' was: "an ecosystem whose species composition and relative abundance have not previously occurred within a given biome." At a subsequent workshop in Brasilia, 2003, various examples of novel ecosystems were discussed. Some centered on disturbances wrought by human intervention, such as the conversion of Cerrado savanna to pasture (Hoffmann and Jackson 2000), and some on indirect consequences of human activities such as increases in non-native species with consequent collapse of 'historical' ecosystems. These examples were numerous, spanned continents and oceans and demonstrated a contemporary outcome of Gleason's individualistic concept as well as a strong linkage between the abiotic and biotic. For instance, Lugo (2004) reported on the growth of alien forests on deforested lands in Puerto Rico; they were eventually re-colonized by native species, but remained dominated by non-natives. These 'new forests' provided important ecological functions, such as the repair of soil structure and fertility and the restoration of forest cover and biodiversity at sites formerly used for production. The disparate threads ultimately coalesced in a seminal paper by Hobbs and colleagues (2006). They defined novel ecosystems as those that exhibit: "(1) novelty: new species combinations with the potential for changes in ecosystem functioning; and (2) human agency: ecosystems that are the result of deliberate or inadvertent human action, but do not depend on continued human intervention for their maintenance". The authors went on to suggest that that it was becoming clear that there were more 'novel' than 'historical' systems, and it was high time that we devoted ecological thought to them.

In subsequent sections we advance from these foundational concepts (i.e. the individualistic concept, the abiotic–biotic tether and pervasive human-caused change) to synthesize the novel ecosystems framework. Using the original Hobbs et al. (2006) components of *novelty* and *human agency* as a starting point, we develop this synthesis by first considering (1) where and how human agency leads to novelty; (2) what level of novelty constitutes a novel ecosystem; and (3) how

human agency acts after a novel ecosystem has emerged.

5.3   SYNTHESIZING THE NOVEL ECOSYSTEMS FRAMEWORK

5.3.1   Human agency as the cause of novelty

Humans now influence all of Earth's ecosystems to some degree, either directly or indirectly (Vitousek et al. 1997; Ellis et al. 2010), and we might therefore conclude that all modern ecosystems are novel (with their higher temperatures and CO_2 concentrations). However, this is not a particularly useful exercise either theoretically or for management (but see Chapter 41 by Marris et al.), and a careful look at the pathways that lead to novelty in ecosystems reveals variation both geographically and with respect to human decision making.

Consider that human effects differ in space. For instance, 'onsite' influences such as development and plantings contrast with 'offsite' influences such as climate change, anthropogenic N deposition or non-native species colonization. In practice, nearly all of Earth's spaces have both onsite and offsite influences occurring simultaneously at some level (Ellis et al. 2010). However, there are examples in which offsite drivers can cause novel ecosystem emergence without onsite activity by humans. For instance, the increasing abundance of lianas in remote areas of tropical forest is one of many compositional changes for which atmospheric CO_2 increases may be a cause (Schnitzer and Bongers 2011). Similarly, climate change is presently altering cryptic Antarctic ecosystems never before visited by humans (Convey and Smith 2006).

Human agency is also expressed through different types of human intent, that is, deliberate versus inadvertent actions. Hawaii was deliberately populated with introduced tree species in the early 20th century in an attempt to foster ecosystem services in heavily logged and burned watersheds (Woodcock 2003). This contrasts with the many inadvertent introductions that afflicted the islands' biodiversity, from avian malaria to argentine ants (Ziegler 2002). Note that most human activity that has unintentionally resulted in the creation of novel ecosystems (as an accidental side-effect) was or is nonetheless intentional activity, undertaken for some other purpose. These actions are

deliberate but the consequent novel ecosystems are an inadvertent result. For instance, Ascension Island is situated in the mid-Atlantic and provided a sanctuary for explorers in the 1500s; they deliberately populated it with goats and sheep and were inadvertently left with an island almost devoid of vegetation (Wilkinson 2004). Additionally, deliberate creation of new ecosystems may be undertaken for various purposes (e.g. 'designer ecosystems', Kueffer and Daehler 2009). This was the remedy selected by botanist Joseph Hooker after stopping off at a barren, goat-nibbled Ascension in 1843, whereupon he began to populate it with foreign plants (Wilkinson 2004).

Hobbs and colleagues (2006) focused on human agency in their effort to differentiate novel ecosystems from other types of ecosystems. They arranged novel ecosystems in the middle of a single axis with 'wild' (or 'historical') ecosystems at one end and intensive agriculture (or other sites intensely managed for human use) at the other (Fig. 5.2), a gradient originally described by Sanderson et al. (2002). Historical ecosystems became novel when subject to invasion (e.g. Weiss 1999), an offsite and inadvertent result of human-caused expansion of species ranges. Similarly, agricultural systems became novel when abandoned (e.g. Lugo 2004), an onsite and inadvertent result of human land use. Importantly, as noted by Kueffer and Daehler (2009), this typology suggests that novel ecosystems are not under direct onsite human control. Put another way, humans do not *prescribe* the abiotic and biotic characteristics of novel ecosystems as they do in agricultural fields, for example. Rather, novel ecosystems are the *response* of the biosphere to human influence.

5.3.2 Novelty versus novel ecosystems

Hobbs et al. (2009) outlined a scheme for identifying historical and novel ecosystems as well as hybrid mixtures of the two, depending on quantifying biotic and abiotic differences from historical ecosystems, namely, novelty (Fig. 3.2). Hobbs et al. (2009) emphasize the second foundational concept behind novel ecosystems, noting that "biotic and abiotic factors often change simultaneously and act synergistically". Indeed, as human influences on biotic or abiotic ecosystem components have increased exponentially, the literature has become festooned with examples of this linkage. Introduced species, for example, are not static additions to the roster of ecological communities; they bring their particular physiologies and life histories to bear on their environment, modifying productivity, soil nutrients and development and physical ecosystem structure among others (e.g. Ehrenfeld 2003; Asner et al. 2008). The door swings both ways, with abiotic changes often facilitating new species colonization or species loss (e.g. MacDougall and Turkington 2005; Wardle et al. 2011).

After how much biotic or abiotic change does something *categorically* become a novel ecosystem? This might be approached in the same way that doctors handle diagnoses. For example, a patient may be diagnosed with a condition if he or she presents with a certain number of symptoms that characterize the condition. Ecosystems might similarly be arrayed according to their degree of novelty in abiotic or biotic factors, and might be deemed 'novel ecosystems' if they exist at sufficient *distance* from either the abiotic or biotic attributes of the historical system (Fig. 5.3). How far a distance? A logical distinction is that the system has crossed a threshold past which any return possibility is a problem of overcoming a strong tendency of the system to remain in its novel state. Consider hysteresis, in which a change in an environmental condition, usually accompanied by positive feedback, leads to the movement of a system to an alternative state (Suding et al. 2004). Even with the reversal of the environmental change, the altered state is maintained well beyond the condition at which the
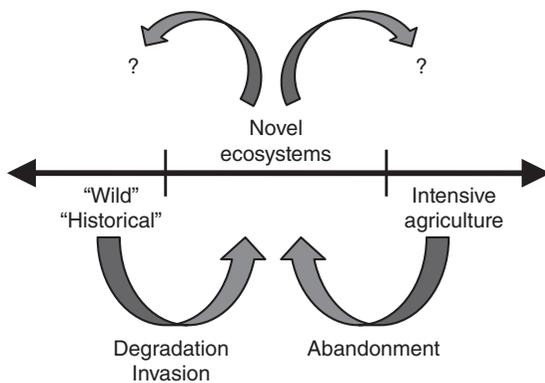
Figure 5.2 Hobbs et al. (2006) made the first attempt at formally defining novel ecosystems, arguing that they arise from either the (1) degradation and invasion of 'wild' or natural/seminatural systems or (2) the abandonment of intensively managed systems. From Hobbs et al. (2006). With permission from John Wiley & Sons.

(a) Theoretical axes of novelty

(b) Applied axes of novelty
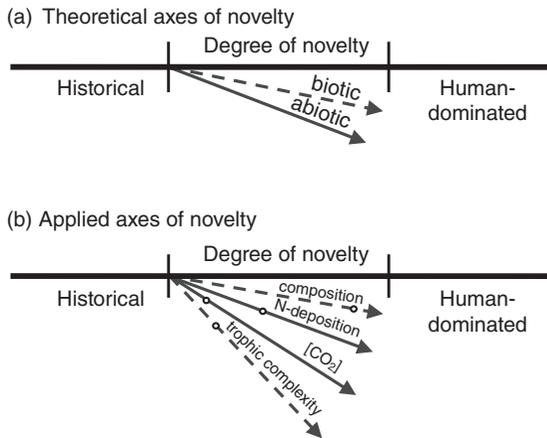
Figure 5.3 A more nuanced view of novelty envisions not a Boolean state, but a quantifiable axis of disparity from the historical condition. (a) Theoretically, this condition can be summarized by biotic and abiotic parts (as depicted in Fig. 3.2) but, (b) in an applied context, either for determination of ecosystem status or informing management, novelty would be measured as the real difference in various abiotic and biotic parameters.

original existed due to negative feedback (e.g. Simenstad et al. 1978). To be a true alternative stable state, exactly the same environmental conditions should lead to alternative states (depending upon initial conditions; Clark et al. 2005) but alternative states may also be observed without hysteresis (Suding and Hobbs 2009). Consider rapid changes in species composition at a tipping point along an environmental gradient, such as alterations to atmospheric N inputs or hydrologic regimes. In such cases, the new community is not stable at the same environmental condition of the old, yet overcoming the massive system-wide inertia of prolonged N deposition or hydrologic change may be impossible.

Hobbs et al. (2009) make a practical distinction between hybrid ecosystems, for which novelty might still practically be reversed (perhaps with great difficulty), and novel ecosystems, for which such reverses are impossible because the ecosystem has crossed an irreversible threshold. The placement of such thresholds with respect to quantitative levels of abiotic or biotic differences from the historical ecosystem might be expected to differ greatly among climates and biomes. For instance, small temperature changes in

boreal latitudes may contribute to melting permafrost (and subsequent ecosystem consequences), whereas the same temperature change may have a more limited influence in temperate latitudes.

Is desirability a factor in differentiating novel ecosystems? We suggest that it should not be. Desirability is a value-based assessment often linked to ecosystems services, and not everyone will place the same value on those services. For example, the Louisiana red-swamp crayfish has been introduced to aquatic systems widely outside its native range. In Kenya it has been implicated in the complete disappearance of native floating and submerged vegetation in Lake Naivasha with significant consequences for the ecosystem (Smart et al. 2002). However, because it decreases the habitat for and preys on native snails that host schistosome flukes, its presence in waterways also results in decreased prevalence of schistosomiasis, an intestinal or urinary disease to which over 12 million Kenyans are susceptible (Mkoji et al. 1999). While admirers of native aquatic plants in Kenya may consider the novelty of crayfish-invaded ecosystems to be highly undesirable, those who are at risk of schistosomiasis may consider it an improvement over the historical state.

5.3.3 Human agency after novelty

Hobbs et al. (2006) argue that human agency must operate as an originating (but not a sustaining) cause of novel ecosystems. This view recognizes the contribution of unrestricted natural selection and new species interactions to novel community assembly and novel ecosystem organization. However, humans also act as managers of novel ecosystems (as addressed in Chapter 3). This raises questions of whether human agency may actually prevent a novel ecosystem from emerging, and how human agency changes novel ecosystems after they have emerged.

Consider agricultural and plantation ecosystems in this context. Are these ecosystems only novel once they have been abandoned, no longer receiving human intervention? Exotic pine plantations are novel assemblages that exist because of deliberate human action and require little human intervention once they have been established. Although they are planted for eventual harvesting, decades will pass during which they may provide novel habitat for native species (Quine and Humphrey 2010). Some may never be harvested (Mascaro 2011). Do we therefore consider them to be

novel ecosystems? If so, can we say the same of an apple orchard or a canola field, which may also provide novel habitat for pollinators and herbivores, but differ in that they have a much shorter time frame over which they do not require maintenance? Where do we draw the line? Invoking Gleason's allergy to classification, we point out that many ecosystems clearly share characteristics of human design and unmanaged novelty.

What occurs when humans undertake restorative action? Consider the framework proposed by Hobbs et al. (2009) in which restoration is directed toward the 'real' historical state (Fig. 3.2), versus that of Kueffer and Daehler (2009) in which restoration is seen as directed toward a historical *analogue* that is perpetuated only by continued human intervention. Importantly, both views agree that classic restoration efforts are directionally opposed to novelty and that beyond a threshold (i.e. in a novel ecosystem) these classic efforts are akin to trying to put the toothpaste back in the tube (see Chapter 3). The views also agree that the restorative action itself constitutes human agency (e.g. by deliberately altering abiotic and biotic attributes). In some instances the level of human agency may be relatively low, particularly when historical ecosystems are well defined and the target ecosystem is not very distant from the historical condition, but there remains a measurable effort needed.

In many systems however, truly recreating a historical analogue (if such a thing can even be defined) is often practically impossible (e.g. riparian ecosystems). At best it would require expensive long-term interventions, very often including engineering (Richardson et al. 2007). Restorations based on this proposition might be viewed as directing ecosystem management toward a fake or inauthentic ecosystem if it is clear that the thing being 'restored' is no more than a list of species that happened to prevail historically on that site (Callicott 2002). Management of such systems for exhibition of the historical parameters may be seen as 'fossilizing' an ecosystem in which the manager is essentially married to an infinite resource commitment, without which the novelty of the system would return. This view suggests that you cannot restore an ecosystem in the same way you can restore a painting (Gunn 1991), and recognizes that self-organization in novel ecosystems may be better tuned to future environmental conditions (Williams and Jackson 2007). Practical considerations are further addressed in other chapters (Chapters 3 and 18), including novel man-agement strategies that approach novel ecosystems with the intent to improve biodiversity, ecosystem function and human welfare, but relax or abandon the notion of returning them to a historical condition (e.g. Hughes et al. 2007; Hobbs et al. 2009).

5.3.4 A novel ecosystems framework

We have argued that the novel ecosystems concept is grounded first in Gleason's individualistic concept that species respond differently when faced with environmental change; ecosystems are therefore not the discrete units they may appear to be. Following this, we devised a *continuous* space in which to ordinate novel ecosystems versus other ecosystems by quantifying the essential components of *novelty* and *human agency* (Fig. 5.4).

In considering novelty, we synthesize two previous iterations: (1) a single axis in which novelty is defined as the abiotic or biotic distance from a historical condition (Fig. 5.4); and (2) two axes, abiotic and biotic, where novel ecosystems occupy the space having high abiotic or biotic distance (or both) from historical ecosystems (Fig. 3.2). Given the second foundational concept behind novel ecosystems (that the biotic and abiotic properties of ecosystems are tethered), we note that the ordination of abiotic *and* biotic axes is not strictly necessary for the purposes of *defining* novel ecosystems (although this retains importance in outlining management approaches and predicting ecosystem function; see Chapter 3). This is implicit in Figure 3.2 (from Hobbs et al. 2009), which shows that novel ecosystems can result from abiotic or biotic novelty or any combination thereof (i.e. they occupy a space equidistant from the origin).

For human agency, we synthesize a gradient of human influence presented by Hobbs et al. 2006 (Fig. 5.2). We follow Kueffer and Daehler (2009) in placing this human agency axis orthogonal to compositional novelty. Here, we specify agency that is 'human design' (deliberate, onsite human activity) where we mean any action by humans to *prescribe* the abiotic or biotic properties of ecosystems. Novelty can therefore occur through human design by way of deliberate, onsite human agency (e.g. land use for agriculture followed by release), inadvertently and away from human design (e.g. the spreading of an introduced species, the uptake of anthropogenic nitrogen) or various combinations of these.
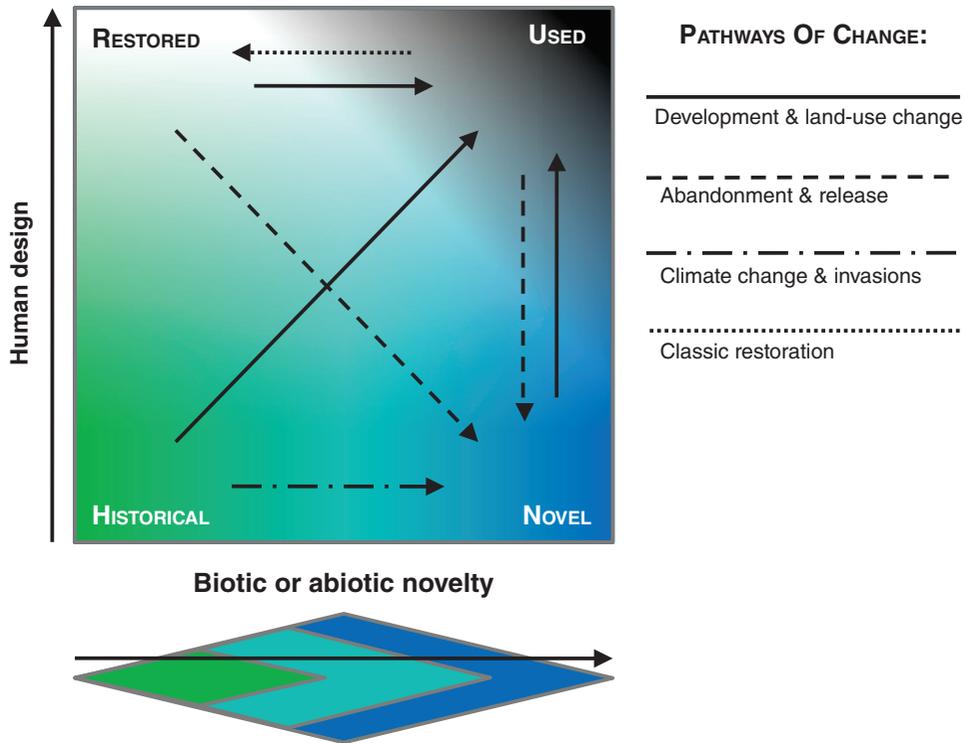
Figure 5.4 The novel ecosystems framework emerges by intersecting quantitative axes for *novelty* and *human design*. As outlined by Hobbs et al. (2009), novelty is the distance in biotic or abiotic properties from the historical state (i.e. note the *x*-axis placement overtop of the Hobbs et al. framework, see Fig. 3.2). Following Kueffer and Daehler (2009), human design represents the onsite, human prescription of abiotic and biotic properties that characterize human-used ecosystems (e.g. lands managed for production) and classic restorations (i.e. to resemble historical composition). The four corners represent absolute states that are rarely (if ever) observed, with the vast majority of real ecosystems contained within. Vectors indicate the 'motion' of a given ecosystem across the state space, and represent various drivers that cause ecosystem change over time. For example, climate change will cause ecosystems to gradually change their abiotic or biotic components, becoming more novel even though human design is absent. By contrast, a corn field is a human-used system which, upon release, may be colonized by new species and become a novel ecosystem. Additional specific examples are shown in Figure 5.5 and described in the text. Reproduced from Hobbs et al. (2009) and Kueffer and Daehler (2009).

The intersection of these two axes mandates four states that are analogous to 'absolute zero'; they are measurable, knowable conditions even though they may be rarely (if ever) observed. Most obviously, historical ecosystems are strictly those never altered by human agency. At the highest level of novelty, we find human-used ecosystems with prescribed abiotic and biotic characteristics that differ from the historical state (e.g. agriculture) as well as novel ecosystems sharing no compositional elements with the historical state, but without onsite human agency to influence their processes.

At the highest levels of human design, both classic restorations and human-used ecosystems share a high level of human intent to control their properties and processes. In the case of agriculture this control is intended to provide for basic human subsistence, while in classic restorations this control is intended to emulate the historical abiotic or biotic composition of an ecosystem. As examples here and in other chapters demonstrate, this level of control reduces the extent to which natural processes may operate (e.g. species sorting, natural selection).

Virtually all real ecosystems will be contained within the state space, often exhibiting elements of multiple ecosystem types. Where the level of compositional novelty and human design can be quantified (e.g. % of introduced species, persons per square mile), an ecosystem's change over time will be depicted by its migration across the space (as a vector). Thresholds within this framework would be annotated along the x axis of novelty, although they would differ according to context. A threshold would therefore keep a given system in a novel state despite attempts to drive its abiotic or biotic characteristics in the direction of a historical ecosystem (negative x direction).

5.3.5   Examples

Lugo (2004) detailed the emergence of novel forests following agricultural abandonment on Puerto Rico (Fig. 5.5a).
1. *Historical tropical moist forest.* Observed only by the first colonists of Puerto Rico, the historical ecosystem includes only indigenous species, many of them endemic to Puerto Rico. Remnants can be seen today within the Luquillio National Forest, although even these forests are no longer strictly historical.
2. *Agricultural development.* Banana, sugar cane and other crops usurp the historical ecosystem, representing the prescription by humans of species composition, ecosystem structure and – to the extent that we can control it – ecosystem function.
3. *Abandonment and colonization by introduced grasses.* A gradual human migration to urban centers results in the abandonment of agricultural fields, releasing these fields from former human prescription of their biotic and abiotic properties. The legacy of human influence remains in the form of altered soil nutrients (Silver et al. 2000) as well as matrix landscapes with agricultural and urban land uses (Lugo and Helmer 2004), and these vacant lands are colonized rapidly by wind-dispersed light-demanding grass species. This initial colonization represents the first appearance of a distinctly novel ecosystem on the site. The composition no longer has any resemblance to the historical tropical moist forest (where grass species were absent).
4. *Succession to introduced trees.* The physical conditions that pervade the grasslands are hostile to the indigenous tree flora but non-native tree species readily colonize and thrive in the open sites, exhibiting novel growth strategies not found in the native flora (e.g. flood and fire tolerance). The sites lack native species and remain compositionally novel, but lose structural novelty as they become forested.
5. *Colonization by native trees in the understory.* The novel forests partially revert in species composition as they are colonized by native trees in the understory. Lugo (2004) observed that after approximately 40 years, basal area is roughly half native and half introduced. Endemic tree species can also be found. Structurally, these forests greatly resemble the historical ecosystem.

Weiss (1999) reviewed the outcome of nitrogen enrichment in serpentine grasslands in California (Fig. 5.5b).
1. *Historical serpentine grasslands.* These grasslands support more than 100 grass and forb species, having low soil N and Ca availability, as well as high heavy metal concentrations. Relic versions remain at the Jasper Ridge Biological Reserve.
**2.** *Anthropogenic N deposition.* Predominately dry N deposition increases N content by as much as 10–30 times historical levels.
3. *Non-native grass colonization.* Introduced grass species (including *Bromus* spp.) thrive under the high N levels and increase in abundance at the expense of native vegetation. In many areas these grass species can attain 100% cover, forming a distinctly novel ecosystem.
**4.** *Novel management.* Grazing by cattle considerably reduces introduced grass species abundances, because cattle preferentially select grasses over forbs. This limited intervention by humans amounts to a minor prescription of species composition (i.e. cattle introduction) that results in a substantial recovery of historical grass and forb composition, even while N levels may remain high.

Other chapters in this volume expand on these examples and consider more, but even these simple examples highlight the complexities of novel ecosystem emergence. In the example of Puerto Rico, it is human land use that is the originating force for novel ecosystem emergence (Fig. 5.5a, position 2). This is a deliberate, onsite human action, after which the novel ecosystem is an inadvertent result of abandonment (Fig. 5.5a, position 3). Here there is a distinct human design pathway, but in California the opposite is the case. Human-caused N deposition is an inadvertent consequence of heavy industry, with offsite effects. Subsequent intervention (Fig. 5.5b, position 4) is a

(a) Novel forests in Puerto Rico
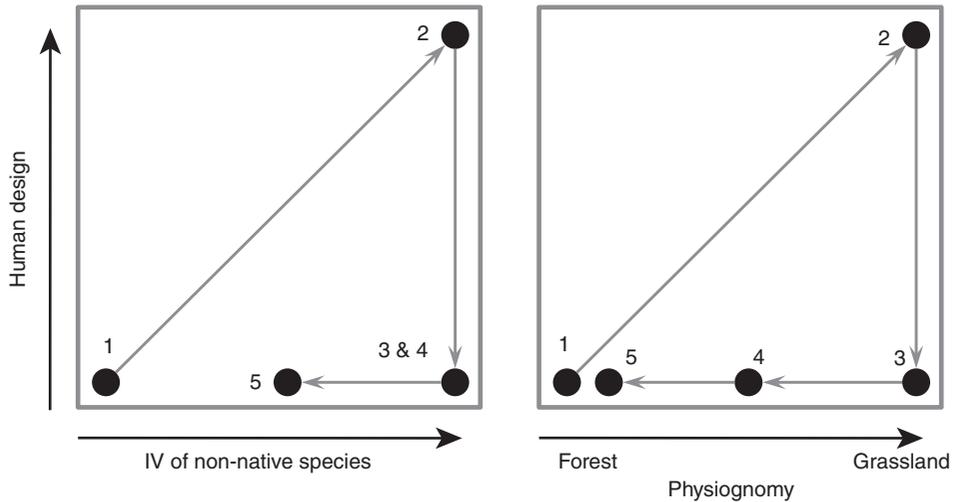
(b) Novel grasslands in California
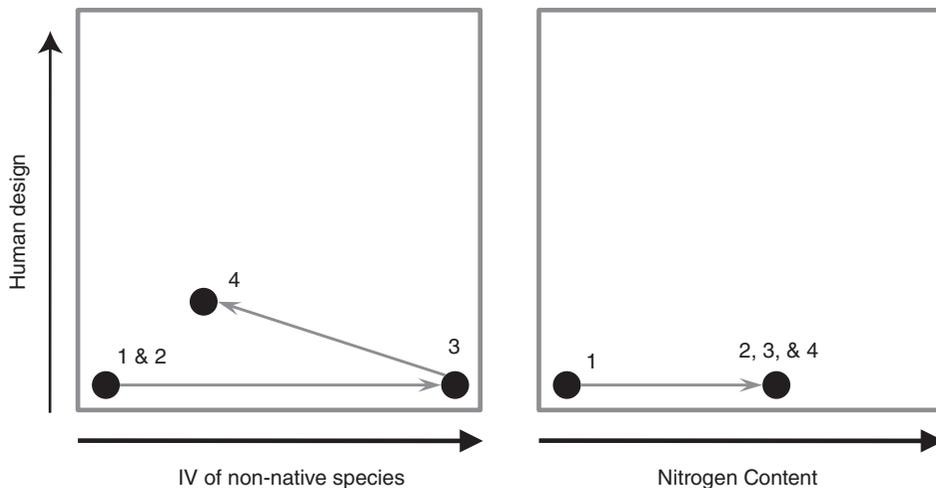
Figure 5.5 Conceptual examples of the emergence of novel ecosystems in (a) Puerto Rico and (b) California. In each case, the left panels highlight changes in biotic properties from historical states (IV is importance value, an index of dominance and density), the right panels highlight an abiotic property (i.e. physical structure in the case of Puerto Rico and N content in the case of California) and the numbers represent different states in time for the same ecosystem in space, as outlined in the text.

design element – albeit a low-impact element of grazing – that creates a system resembling, but not the same as, that which prevailed historically. The conceptual framework (Fig. 5.4) suggests that a classic restoration which would disallow cattle (a non-native species) would require a greater human design effort.

The tether between abiotic and biotic factors is also revealed. In Puerto Rico, introduced grass species result in a high level of structural novelty, forming a grassland where one did not exist (Fig. 5.5a, position 3). Further, while the penultimate novel forest maintains a high level of compositional novelty, it loses

structural novelty as it is colonized by introduced tree species and becomes a tropical forest again (Fig. 5.5a, position 4).

5.4   CONCLUSIONS

Earth's communities and ecosystems have disassembled and emerged anew in the wake of environmental upheavals throughout the planet's history. In the past, these changes were driven by asteroids, volcanoes, glaciers and the rise and fall of oceans and mountains. Today, humans are driving extensive and pervasive change, and novel ecosystems are the unambiguous response.

The debate elucidated in this chapter highlights the perils of a one-sentence definition for novel ecosystems. Indeed, we have shown that even as the formal concept of a novel ecosystem has developed over time (Milton 2003; Lugo 2004; Hobbs et al. 2006; Hobbs et al. 2009; Kueffer and Daehler 2009), a precise declaration has not been forthcoming. On theoretical grounds (vis-à-vis Gleason), we advocate strongly for a continuous understanding (Fig. 5.4). Nevertheless, it is important that we appreciate that we are living in a changing world and that societal restoration norms of systems with historical species composition may not be a suitable or even possible future intervention target. In these landscapes, the existence of novel ecosystems must be recognized and their future management debated. Here, a categorical definition can have considerable utility.

Based on the framework proposed, for a given space on the Earth's surface, a *novel ecosystem* is not: (1) a system that would have occupied that space in the past (i.e. part of a historical range of variability); (2) managed intensively for specific production or built over; or (3) managed with the purpose of reproducing the historical ecosystem (i.e. classic restoration).

A novel ecosystem is one of abiotic, biotic and social components (and their interactions) that, by virtue of human influence, differ from those that prevailed historically, having a tendency to self-organize and manifest novel qualities without intensive human management. Novel ecosystems are distinguished from hybrid ecosystems by practical limitations (a combination of ecological, environmental and social thresholds) on the recovery of historical qualities.

This definition is considered further in the following chapter, and we reflect on how it adds to the eco-logical, environmental and management lexicon moving forward.

REFERENCES

Asner, G.P., Hughes, R.F., Vitousek, P.M., Knapp, D.E., Kennedy-Bowdoin, T., Boardman, J., Martin, R.E., Eastwood, M. and Green, R.O. (2008) Invasive plants transform the three-dimensional structure of rain forests. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 4519–4523.

Behrensmeyer, A.K., Damuth, J.D., Dimichele, W.A., Potts, R., Sues, H.-D. and Wing, S.L. (1992) *Terrestrial Ecosystems Through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals*. University of Chicago Press, Chicago, IL.

Callicott, J.B. (2002) Choosing appropriate temporal and spatial scales for ecological restoration. *Journal of Bioscience*, **27**, 409–420.

Chapin, F.S. III and Starfield, A.M. (1997) Time lags and novel ecosystems in response to transient climatic change in artic Alaska. *Climatic Change*, **35**, 449–461.

Clark, B.R., Hartley, S.E., Suding, K.N. and De Mazancourt, C. (2005) The effect of recycling on plant competitive hierarchies. *American Naturalist*, **165**, 609–622.

Clark, D.A., Piper, S.C., Keeling, C.D. and Clark, D.B. (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 5852–5857.

Clements, F.E. (1916) *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institute of Washington, Washington, D.C.

Convey, P. and Smith, R.I.L. (2006) Responses of terrestrial Antarctic ecosystems to climate change. *Plant Ecology*, **182**, 1–10.

Cordes, E.E., Bergquist, D.C., Shea, K. and Fisher, C.R. (2003) Hydrogen sulphide demand of long-lived vestimentiferan tube worm aggregations modifies the chemical environment at deep-sea hydrocarbon seeps. *Ecology Letters*, **6**, 212–219.

Davis, M.B. (1981) Quaternary history and the stability of forest communities, in *Forest Succession: Concepts and Applications* (eds D.C. West, H.H. Shugart and D.B. Botkin), Springer-Verlag, New York, NY, USA, 134–153.

Davis, M.B. (1983) Quaternary history of deciduous forests of Eastern North America and Europe. *Annals of the Missouri Botanical Garden*, **70**, 550–563.

Delcourt, H.R. (2002) *Forests in Peril: Tracking Deciduous Trees from Ice-Age Refuges into the Greenhouse World*. The McDonald and Woodward Publishing Company, Blacksburg, VA.

Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503–523.

Ellis, E.C., Goldewijk, K.K., Siebert, S., Lightman, D. and Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, **19**, 586–606.

Gleason, H.A. (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, **53**, 7–27.

Gunn, A.S. (1991) The restoration of species and natural environments. *Environmental Ethics*, **13**, 291–310.

Hobbs, R.J., Arico, S., Aronson, J., Brown, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R. and Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology & Biogeography*, **15**, 1–7.

Hobbs, R.J., Higgs, E. and Harris, J.A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution*, **24**, 599–605.

Hoffmann, W.A. and Jackson, R.B. (2000) Vegetation-climate feedbacks in the conversion of tropical savanna to grassland. *Journal of Climate*, **13**, 1593–1602.

Hughes, T.R., Rodriques, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., Mccook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S. and Willis, B. (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, **17**, 360–365.

Jackson, S.T. (2006) Vegetation, environment, and time: the origination and termination of ecosystems. *Journal of Vegetation Science*, **17**, 549–557.

Janzen, D.H. (1985) On ecological fitting. *Oikos*, **45**(3), 308–310.

Jenny, H. (1941) *Factors of Soil Formation: A System of Quantitative Pedology*. McGraw-Hill, New York, NY, USA.

Jenny, H. (1980) *The Soil Resource: Origin and Behavior*. Springer-Verlag, New York, NY, USA.

Kueffer, C. and Daehler, C.C. (2009) A habitat-classification framework and typology for understanding, valuing, and managing invasive species impacts, in *Management of Invasive Weeds* (ed. Inderjit), Springer Science and Business Media BV, 77–101.

Lugo, A.E. (2004) The outcome of alien tree invasions in Puerto Rico. *Frontiers in Ecology and the Environment*, **2**, 265–273.

Lugo, A.E. and Helmer, E. (2004) Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management*, **190**, 145–161.

MacDougall, A.S. and Turkington, R. (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, **86**, 42–55.

Mascaro, J. (2011) Eighty years of succession in a non-commercial plantation on Hawai'i Island: are native species returning? *Pacific Science*, **65**, 1–15.

McIntosh, R.P. (1975) H.A. Gleason: 'Individualistic Ecologist' 1882–1975: His contributions to ecological theory. *Bulletin of the Torrey Botanical Club*, **102**, 253–273.

Milton, S.J. (2003) 'Emerging ecosystems': a washing-stone for ecologists, economists and sociologists? *South African Journal of Science*, **99**, 404–406.

Mkoji, G.M., Hofkin, B.V., Kuris, A.M., Stewart-Oaten, A., Mungai, B.N., Kihara, J.H., Mungai, F., Yundu, J., Mbui, J., Rashid, J.R., Kariuki, C.H., Ouma, J.H., Koech, D.K. and Loker, E.S. (1999) Impact of the crayfish *Procambarus clarkii* on *Schistosoma haematobium* transmission in Kenya. *American Journal of Tropical Medicine and Hygine*, **61**, 751–759.

Naeem, S. (2002) Ecosystem consequences of biodiversity loss: The evolution of a paradigm. *Ecology*, **83**, 1537–1552.

Odum, E.P. (1969) The strategy of ecosystem development. *Science*, **164**, 262–270.

Pagani, M., Arthur, M.A. and Freeman, K.H. (1999) Miocene evolution of atmospheric carbon dioxide. *Paleoceanography*, **14**, 273–292.

Pielou, E.C. (1991) *After the Ice Age: The Return of Life to Glaciated North America*. The University of Chicago Press, Chicago, IL, USA.

Quine, C.P. and Humphrey, J.W. (2010) Plantations of exotic tree species in Britain: irrelevant for biodiversity or novel habitat for native species? *Biodiversity and Conservation*, **19**, 1503–1512.

Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromber, J.C., Kirkman, S.P., Pysek, P. and Hobbs, R.J. (2007) Riparian vegetation: degradation, alien plant invasions, and restoration projects. *Diversity and Distributions*, **13**, 126–139.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redfrod, K.H., Wannebo, A.V. and Woolmer, G. (2002) The human footprint and the last of the wild. *BioScience*, **52**, 891–904.

Schnitzer, S.A. and Bongers, F. (2011) Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters*, **14**, 397–406.

Silver, W.L., Ostertag, R. and Lugo, A.E. (2000) The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. *Restoration Ecology*, **8**, 394–407.

Simenstad, C.A., Estes, J.A. and Kenyon, K.W. (1978) Aleuts, sea otters, and alternative stable-state communities. *Science*, **200**, 403–411.

Smart, A.C., Harper, D.M., Malaisse, F., Schmitz, S., Coley, S. and Gouder De Beauregard, A.-C. (2002) Feeding of the exotic Louisiana red swamp crayfish, Procambarus clarkii (Custacea, Decapoda), in an African tropical lake: Lake Naivasha, Kenya. *Hydrobiologia*, **488**, 129–142.

Suding, K.N. and Hobbs, R.J. (2009) Threshold models in restoration and conservation: a developing framework. *Trends in Ecology & Evolution*, **24**, 271–279.

Suding, K.N., Gross, K.L. and Houseman, G.R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, **19**, 46–53.

Tansley, A.G. (1935) The use and abuse of vegetational concepts and terms. *Ecology*, **16**, 284–307.

Vermeij, G.J. (2005) Invasion as expectation: a historical fact of life, in *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (eds D.F. Sax, J.J. Stachowicz and S.D. Gaines), Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, 315–340.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. and Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.

Wardle, D.A., Bargett, R.D., Callaway, R.M. and Van Der Putten, W.H. (2011) Terrestrial ecosystem responses to species gains and losses. *Science*, **332**, 1273–1277.

Weiss, S.B. (1999) Cars, cows, and checkerspot butterflies: nitrogen deposition and managment of nutrient-poor grasslands for a threatened species. *Conservation Biology*, **13**, 1476–1486.

Wilkinson, D.M. (2004) The parable of Green Mountain: Ascension Island, ecosystem construction, and ecological fitting. *Journal of Biogeography*, **31**, 1–4.

Williams, J.W. and Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.

Woodcock, D. (2003) To restore the watersheds: Early twentieth-century tree planting in Hawai'i. *Annals of the Association of American Geographers*, **93**, 624–635.

Ziegler, A.C. (2002) *Hawaiian Natural History and Evolution.* University of Hawai'i Press, Honolulu, HI, USA.