



Novel ecosystems: theoretical and management aspects of the new ecological world order

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ABSTRACT

We explore the issues relevant to those types of ecosystems containing new combinations of species that arise through human action, environmental change, and the impacts of the deliberate and inadvertent introduction of species from other regions. Novel ecosystems (also termed ‘emerging ecosystems’) result when species occur in combinations and relative abundances that have not occurred previously within a given biome. Key characteristics are novelty, in the form of new species combinations and the potential for changes in ecosystem functioning, and human agency, in that these ecosystems are the result of deliberate or inadvertent human action. As more of the Earth becomes transformed by human actions, novel ecosystems increase in importance, but are relatively little studied. Either the degradation or invasion of native or ‘wild’ ecosystems or the abandonment of intensively managed systems can result in the formation of these novel systems. Important considerations are whether these new systems are persistent and what values they may have. It is likely that it may be very difficult or costly to return such systems to their previous state, and hence consideration needs to be given to developing appropriate management goals and approaches.

Keyword

Biological invasions, degradation, ecosystem transformation, land abandonment, novel ecosystem.

INTRODUCTION

‘Synthetic ecosystems include conditions and combinations of organisms never before in existence (Odum, 1962)’

Most of the world’s ecosystems are now impacted by humans to a greater or lesser extent (Vitousek *et al.*, 1997; Sanderson *et al.*, 2002), and humans thus play an important role in modifying or regulating the types and rates of ecosystem

change. In addition, global trading has breached biogeographical boundaries and facilitated the spread of species into regions that they would probably never have reached under normal conditions (Jenkins, 1996; French, 2000; McNeely, 2000). This paper considers those types of ecosystems containing new combinations of species that arise through human action, environmental change, and the impacts of the deliberate and inadvertent introduction of species from other parts of the world.

WHY NOVEL ECOSYSTEMS?

Novel ecosystems (also termed ‘emerging ecosystems’, e.g. see Milton, 2003) have species compositions and relative abundances that have not occurred previously within a given biome. The key characteristics are (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. Such ecosystems result from biotic response to human-induced abiotic conditions and/or novel biotic elements (e.g. land degradation, enrichment of soil fertility, introduction of invasive species). This includes the cessation of management of systems that have been managed or created by humans (e.g. agroforestry systems, pastoral land). New species combinations arise frequently in today’s world in conditions of strong direct or indirect human impact. In particular, there are three main reasons for their existence.

- 1 Human impact has resulted in local extinction of most of the original animal, plant and microbial populations and/or the introduction of a suite of species not previously present in that biogeographical region.
- 2 Predominating urban, cultivated or degraded landscapes around target ecosystems create dispersal barriers for many animal, plant and microbial species.
- 3 Direct (e.g. removal of natural soil, dam construction, harvesting, pollution) and indirect (e.g. erosion due to lack of vegetation or overgrazing) human impact has resulted either in major changes in the abiotic environment or a decrease in the original propagule species pool, both of which can prevent the re-establishment of pre-existing species assemblages.

These types of ecosystem can be thought of as occupying a zone somewhere in the middle of the gradient between ‘natural’ or ‘wild’ ecosystems, on one hand, and intensively managed systems on the other hand [Fig. 1; see Sanderson *et al.* (2002) for a discussion of this gradient]. Clearly, the proportion of each broad type of ecosystem will vary from place to place, and the situation is dynamic as natural areas are modified and intensive agriculture increases in some places, while in others agricultural land is abandoned.

Under what sort of conditions will novel ecosystems occur? Clearly, there are many different biomes in the world, the distribution of which is determined primarily by climate (e.g. Holdridge, 1947, 1967). Environmental harshness will vary across life zones, depending on temperature, fertility and moisture availability. Ewel (1999) suggested that abiotic stress was likely to display a nonlinear relationship with environmental harshness (Fig. 2a); similarly, as environmental harshness declines, the opportunity increases for either more species to grow and thrive or for particular species to become dominant, leading to increased competition and predation, which Ewel aggregated into ‘biotic stress’.

If abiotic and biotic stresses are combined, total stress is greatest at either end of the gradient: in harsh environments the constraints to establishment and/or growth are primarily abiotic, while in more benign environments the constraints are mainly biotic, arising from the pre-existing mix of species present. The inverse

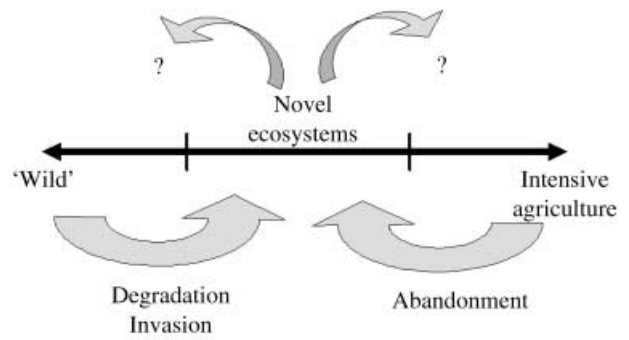


Figure 1 Novel ecosystems arise either from the degradation and invasion of ‘wild’ or natural/seminatural systems or from the abandonment of intensively managed systems.

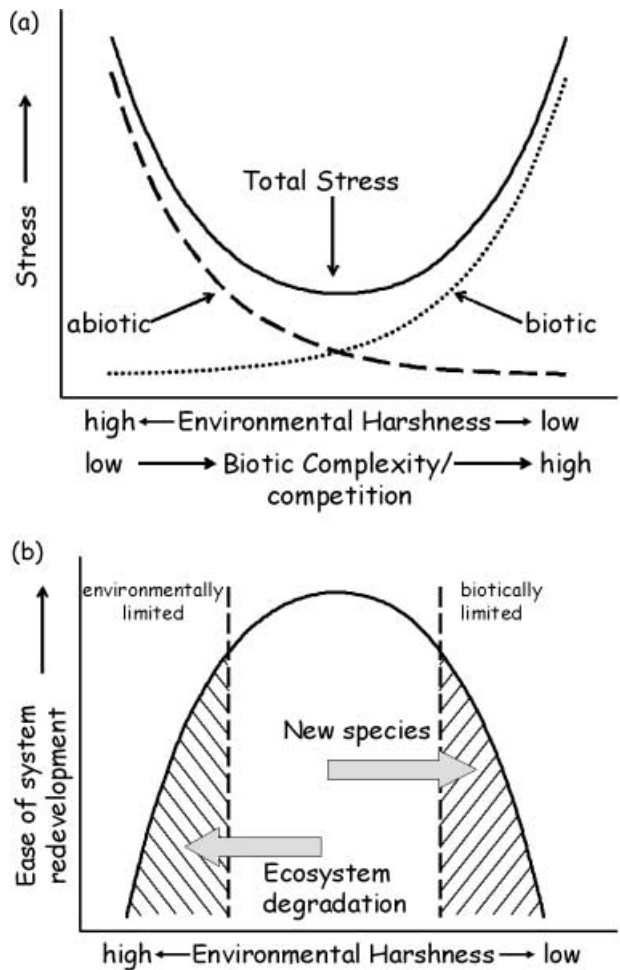


Figure 2 (a) Stress on an ecosystem is related to environmental harshness and biotic complexity: in harsh environments the constraints to establishment and/or growth are primarily abiotic, while in more benign environments the constraints are mainly biotic, arising from the pre-existing mix of species present. Total stress is greatest at either end of the gradient. The inverse image of this graph (b) portrays the ease with which an ecosystem will redevelop following disturbance or human modification. Ecosystem degradation leads to more abiotic stress, while the addition of new species leads to more biotic stress, and ecosystem redevelopment is less likely in both cases (after Ewel, 1999; see also Menge & Sutherland, 1987; Bertness & Callaway, 1994).

image of this graph (Fig. 2b) can be considered to describe the ease with which an ecosystem will redevelop following disturbance or human modification. Because aggregate stress is lowest in the mid-range of the *x*-axis, ecosystem redevelopment can be hypothesized to occur with most ease in this region. Redevelopment to a pre-existing composition can be expected to be limited by abiotic conditions at one end of the graph and biotic conditions at the other. Human activities increasingly either degrade ecosystems, leading to harsher abiotic conditions and/or more limited dispersal of the species originally present, or introduce new species which alter the biotic environment and potentially reduce the potential for system redevelopment. In both of these situations, novel ecosystems can be expected.

TEMPORAL AND SPATIAL SCALES

All ecosystems are naturally dynamic; many parts of the world have had human inhabitation for millennia, and there is increasing recognition of the likely impacts of humans on ecosystems over large time-frames (e.g. Redman, 1999; Lentz, 2000). The transport of species across the world has also been happening for centuries (e.g. Sauer, 1988; Clark, 2000). Hence the opportunity for novel ecosystems to develop has been available for a long time. For instance, in areas such as the Mediterranean Basin most ecosystems are heavily transformed and composed of species having different biogeographical origins (Blondel & Aronson, 1995). In addition, there are documented examples of deliberate 'ecosystem construction' from various historical periods: for instance, the introduction of species to Ascension Island which led to the formation of an entirely novel forest type (Wilkinson, 2004). Our current concern with novel ecosystems must thus be set in a longer time-frame, and questions of relative value compared with other ecosystem types should perhaps focus on the services either provided by or lost from particular types of ecosystem. It is, however, clear that rates of change are much faster in modern times and that, for better or for worse, new technologies help to overcome biogeographical and biophysical barriers to establishment.

Spatial scale is also an important consideration, and ecosystems need to be considered within a landscape context. Many parts of the world are now a patchwork of different land uses and ecosystems ranging across the 'natural' to 'intensively managed' gradient. A particular ecosystem within this patchwork has both intrinsic and contextual characteristics. The dynamics of an emerging ecosystem are determined to some extent by the transport of propagules and movement of organisms across the landscape, and in turn the ecosystem may act as a source of propagules that move into less modified areas.

SYSTEM THRESHOLDS

An important question is whether novel ecosystems can be considered to have crossed a threshold to a new or different state, which could either be transient or stable. This question requires further consideration, perhaps in the light of current discussions of thresholds in a restoration–ecology context (Hobbs & Norton, 1996; Whisenant, 1999; Hobbs & Harris, 2001). We emphasize

here that we are not discussing simply changes to another alternative stable state within natural ecosystems, but rather changes to an entirely new state caused, for instance, by the invasion by entirely new sets of species.

In principle, there are two types of threshold that ecosystems can cross. *Biotic thresholds* are created by dispersal barriers and result in unusual combinations of species and functional groups arise. *Abiotic thresholds* result from severely changed abiotic conditions such as, for example, soil erosion on clearcut or over-grazed slopes, or different hydrological conditions due to changed evapotranspiration. These result in novel abiotic conditions where species from the original natural ecosystem cannot establish, even when dispersal barriers are crossed (Vitousek *et al.*, 1997; Levine *et al.*, 2003).

In some cases, major changes in the local environment may also arise due to the invasion of new species that prevent the growth and regeneration of pre-existing species by competition or predation or by causing changes in ecosystem functioning, including disturbance regime. This may then leave a legacy of system change that remains even if the species is removed. There are also cases where the removal of the target invaders allows other invasive species to move in and alter the ecosystem even more (Zavaleta *et al.*, 2001).

EXAMPLES

There is a range of situations in which novel ecosystems can occur. Examples include the following.

- Alien pine species (*Pinus halepensis*, *P. pinaster* and *P. radiata*) invade and transform the species-rich fire-prone fynbos shrublands in South Africa's Cape Floristic Region (Cowling, 1992; Richardson & Cowling, 1992; Richardson *et al.*, 1996). The pines, which have serotinous cones, colonize fynbos after fires. The aliens initially behave in a similar manner to the native shrubs, but their short juvenile periods and large reserves of highly mobile seeds buffer them against fire-induced population crashes. The natural nonequilibrium system is disrupted, and cyclical replacement of native shrubs is prevented. As the invaders proliferate after each fire, competition with fynbos elements is intensified, leading eventually to the local extinction of the natives as residual seed stores are depleted. There is no cyclical replacement without human intervention (such as felling of pines), and a depauperate steady-state results (Richardson & Cowling, 1992).
- The rain-shadow tussock grasslands of New Zealand have been induced by cultural activities and have almost certainly crossed ecological thresholds that in most cases will be difficult to reverse. Prior to human settlement, New Zealand was forested almost totally below the treeline. With Polynesian settlement around 1200–1300 AD extensive areas of forest were burnt, especially in the rain-shadow areas of the eastern South Island. While some regeneration towards forest occurred, the almost complete removal of forest coupled with the difficult climate (cold and dry) and ongoing fire maintained tussock grassland and shrubland communities in most areas. European settlement (1850s onwards) brought extensive pastoralism to these grasslands,

Table 1 Other examples of novel ecosystems, indicating the breadth of ecosystem types involved and the range of causal factors leading to the novel system, and giving relevant literature sources. The list is not intended to be comprehensive, but merely to indicate the pervasiveness of novel ecosystems

Ecosystem type	Description	Reference
Puerto Rico's 'new' forests	Regenerating forests on degraded lands, composed largely of non-native species and exhibiting multiple successional pathways	Aide <i>et al.</i> , 1996; Zimmerman <i>et al.</i> , 2000; Lugo, 2004
Brazil's tropical savannas (the Cerrado)	Savannas transformed extensively by increased fire and introduction of grass species such as <i>Melinis minutiflora</i>	Hoffmann & Jackson, 2000; Klink & Moreira, 2002
Mediterranean pine woodlands	Woodlands with altered dynamics due to changing climatic conditions coupled with altitudinal range shifts in herbivores	Peñuelas <i>et al.</i> , 2002; Hodar <i>et al.</i> , 2003
Rivers in the Western United States	Rivers altered by regulation, altered flows and invasive species	Scott & Lesch, 1996; Ward & Stanford, 1979; Postel <i>et al.</i> , 1998; Kowalewski <i>et al.</i> , 2000
Tropical agroforestry systems	Diverse combinations of native and non-native perennial plants used locally to derive ecosystem goods and services	Ewel <i>et al.</i> , 1991; Ewel, 1999
Kelp forests	Removal of keystone species (sea otter) results in shift to novel ecosystem state	Simenstad <i>et al.</i> , 1987; Estes & Duggins, 1995
Near-shore ocean floors invaded by <i>Caulerpa</i>	Invasion by the alga <i>Caulerpa</i> in the Mediterranean and elsewhere leads to a novel ecosystem and monospecific dominance	Davis <i>et al.</i> , 1997; Meinesz, 1999
San Francisco Bay	An estuary now dominated almost entirely by non-native species, with entirely novel species combinations	Carlton, 1989; Cohen & Carlton, 1998

with more frequent fire and heavy grazing (especially by sheep, but also by rabbits) leading to a compositional shift in many areas from tall tussocks (*Chionochloa* species) to short tussocks (*Festuca* and *Poa* species). More recently, invasive plants (herbaceous and woody) have become increasing dominant and compositional change appears to be ongoing irrespective of management practices (Treskonova, 1991; Duncan *et al.*, 2001). Tussock grasslands are now a highly valued ecosystem in New Zealand, and there are active attempts to maintain or restore grasslands for conservation purposes.

- Secondary salinization in southern Australia leads to the replacement of pre-existing native vegetation with an impoverished, alien-dominated vegetation. The breakdown of the natural hydrological equilibrium and the subsequent salinization of the soil profile, combined with the extended periods of waterlogging associated frequently with shallow water tables, generally forces vegetation across a transitional threshold to a new stable state characterized by severe reductions in biodiversity. Rich and structurally diverse vegetation assemblages are replaced by a small number of native chenopods and salt-tolerant alien species. The extreme abiotic stress posed by the combination of soil salinity and waterlogging prevents the recruitment and survival of all but the most stress-tolerant of plant species. Further, the highly fragmented nature of native vegetation in the agricultural districts where secondary salinity is a problem provides further barriers to propagule dispersal into areas affected by salinity (Cramer & Hobbs, 2002).

Further examples are listed briefly in Table 1 to indicate the wide range of situations in which 'novel' ecosystems can emerge.

DISCUSSION

Often, in cases such as those outlined above, the biotic composition of an ecosystem has undergone change to a new relatively stable state. This change has come about either through proximate changes in management or because of broader-scale environmental changes. Changes in plant–animal interactions, biogeochemistry and disturbance frequencies can all be important. Frequently some sort of positive feedback loop occurs where the members of the novel ecosystem facilitate the maintenance (and sometimes spread) of that ecosystem and inhibit restoration of the previous system. The development of novel ecosystems has occurred in similar ways in different parts of the world — this probably represents some sort of 'convergence' through homogenization of biotas and parallel activities of humans aimed at shaping ecosystems to their own purposes. In fact, the replacement of many local species with a relatively small number of widespread weedy species is likely to produce much more spatially homogenized novel ecosystems (McKinney & Lockwood, 1999; Olden *et al.*, 2004).

New biotic assemblages affect key interactions and processes, such as plant–animal interactions, microbial communities breaking down organic matter in soils, and the impacts and reaction to increasing soil salinity. Key questions for the future are how we develop management schemes that maximize beneficial changes and reduce the less beneficial aspects (which also depend on how and by whom 'benefit' is defined). Because novel ecosystems result from human actions, management is required to guide their development. How we manage these new ecosystems effectively is a point for debate: what should the goals be and how should

these systems fit with other systems along the wild–intensively managed gradient? If the system is transient, how do we guide it along a particular trajectory? If it is stable, can we manage it effectively to gain benefit from its current state or devise effective methods of directing it to a new, more preferable state? It is certainly clear that these systems will be very difficult, if not impossible, to return to some ‘more natural’ state in terms of time, effort and money. This is a very important point as it argues simultaneously for (1) conserving less impacted places now so they do not change into some new, possibly less desirable, form; and (2) not wasting precious resources on what may be a hopeless quest to ‘fix’ those systems for which there is little chance of recovery back to some pre-existing condition. Rather, we should perhaps accept them for what they are and what benefits they provide.

This may seem to some to be a defeatist approach which recognizes that some ecosystems are more or less transformed irreversibly and that invasive species are likely to persist in some cases. Indeed, comments from reviewers of the draft manuscript indicated a lack of willingness to accept such ecosystems as a legitimate target for ecological thought or management action. For instance, one reviewer commented that the examples are ecological disasters, where biodiversity has been decimated and ecosystem functions are in tatters, and that ‘it is hard to make lemonade out of these lemons’.

Our point is, however, that we are heading towards a situation where there are more lemons than lemonade, and we need to recognize this and determine what to do with the lemons. We suggest that the approach is simply pragmatic and provides a way for prioritizing scarce conservation and management resources. As Redford & Richter (1999) discuss, there is a variety of ways in which humans and ecosystems interact, and novel ecosystems are likely to have some useful kinds of functions, while not others. We should perhaps move away from the one-dimensional dichotomy between natural and human dominated towards a more effective depiction of how human beings interact with nature.

Many questions remain to be explored more fully. For instance:

- 1 Are novel ecosystems on the increase? Will such ecosystems predominate at the end of the present century? What does this mean for our attempts to conserve ‘wild’ or ‘natural’ ecosystems?
- 2 Do we need special concepts and methods to approach today’s novel ecosystems or do they simply represent one quite typical example of ecosystem dynamics that have always occurred?
- 3 Are new species combinations provoking ‘new’ ecosystem functioning or properties? To what extent will a new combination of species maintain similar functional properties with respect to the old species pool (i.e. is there functional redundancy or are new properties added)?
- 4 To what extent do these new species combinations alter the original network of mutualistic and antagonistic interactions, and what are the consequences for community organization?
- 5 Can we recognize thresholds in ecosystems and landscapes?
- 6 How do novel ecosystems affect the relative values of ‘natural’ and managed systems?

7 How does the concept of novel ecosystems relate to the marine environment?

8 What are the important socio-economic aspects that need to be considered in relation to novel ecosystems?

Regardless of the details of the debate, it is clear that humans all over the planet are assisting with the development of new ecosystems. Such ecosystems are not emerging *de novo*. Instead they are emerging from ‘within’ pre-existing systems that are naturally dynamic, both over long and short time-scales. We need to consider how best to manage these ecosystems, and utilize them for benefit to society — both as individual ecosystems and in their broader landscape context.

ACKNOWLEDGEMENTS

We dedicate this paper to Howard T. Odum. This paper developed from discussions at a workshop in Granada in September 2002, during which news came through of H. T.’s death on 11 September 2002. Several workshop participants were Odum’s students. We also thank UNESCO/MAB and SCOPE for financial support for the workshop, Regino Zamora and his team in Granada for providing such a pleasant and stimulating venue for the workshop, and several anonymous reviewers for critical feedback on the draft manuscript.

REFERENCES

- Aide, T.M., Zimmerman, J.K., Rosario, M. & Marcano, H. (1996) Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica*, **28**, 537–548.
- Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.
- Blondel, J. & Aronson, J. (1995) Biodiversity and ecosystem function in the Mediterranean Basin: human and non-human determinants. *Mediterranean-type ecosystems: the function of biodiversity* (ed. by G.W. Davis and D.M. Richardson), pp. 43–119. *Ecological Studies*, Vol. 109. Springer-Verlag, Berlin.
- Carlton, J.T. (1989) Man’s role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conservation Biology*, **3**, 265–273.
- Clark, R.P. (2000) *Global life systems: Population, food and disease in the process of globalization*. Rowman and Littlefield, Lanham.
- Cohen, A.N. & Carlton, J.T. (1998) Accelerating invasion rate in a highly invaded estuary. *Science*, **279**, 555–557.
- Cowling, R.M. (1992) *The ecology of fynbos: nutrients, fire and diversity*. Oxford University Press, Cape Town.
- Cramer, V.A. & Hobbs, R.J. (2002) Ecological consequences of altered hydrological regimes in fragmented ecosystems in southern Australia: impacts and possible management responses. *Austral Ecology*, **27**, 546–564.
- Davis, A.R., Roberts, D.E. & Cummins, S.P. (1997) Rapid invasion of a sponge-dominated deep-reef by *Caulerpa scalpelliformis* (Chlorophyta) in Botany Bay, New South Wales. *Australian Journal of Ecology*, **22**, 146–150.

- Duncan, R.P., Webster, R.J. & Jensen, C.A. (2001) Declining plant species richness in the tussock grasslands of Canterbury and Otago, South Island, New Zealand. *New Zealand Journal of Ecology*, **25**, 35–47.
- Estes, J.A. & Duggins, D.O. (1995) Sea otters and kelp forests in Alaska: generality and variation in a community paradigm. *Ecological Monographs*, **65**, 75–100.
- Ewel, J.J. (1999) Natural systems as models for the design of sustainable systems of land use. *Agroforestry Systems*, **45**, 1–21.
- Ewel, J.J., Mazzarino, M.J. & Berish, C.W. (1991) Tropical soil fertility changes under monocultures and successional communities of different structure. *Ecological Applications*, **1**, 289–302.
- French, H. (2000) *Vanishing borders: protecting the planet in the age of globalization*. W.W. Norton and Company, New York.
- Hobbs, R.J. & Harris, J.A. (2001) Restoration ecology: repairing the Earth's ecosystems in the new millennium. *Restoration Ecology*, **9**, 239–246.
- Hobbs, R.J. & Norton, D.A. (1996) Towards a conceptual framework for restoration ecology. *Restoration Ecology*, **4**, 93–110.
- Hodar, J.A., Castro, J. & Zamora, R. (2003) Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. *Biological Conservation*, **110**, 123–129.
- Hoffmann, W.A. & Jackson, R.B. (2000) Vegetation–climate feedbacks in the conversion of tropical savanna to grassland. *Journal of Climate*, **13**, 1593–1602.
- Holdridge, L.R. (1947) Determination of world plant formations from simple climate data. *Science*, **105**, 367–368.
- Holdridge, L.R. (1967) *Life zone ecology* (revised edn). Tropical Science Centre, San Jose, Costa Rica.
- Jenkins, P.T. (1996) Free trade and exotic species introductions. *Conservation Biology*, **10**, 300–302.
- Klink, C.A. & Moreira, A.C. (2002) Past and current human occupation, and land use. *The cerrados of Brazil: ecology and natural history of a neotropical savanna* (ed. by P.S. Oliveira and R.J. Marquis), pp. 69–75. Columbia University Press, New York.
- Kowalewski, M., Serrano, G.A., Flessa, K.W. & Goodfriend, G.A. (2000) Dead delta's former productivity: two trillion shells at the mouth of the Colorado River. *Geology*, **28**, 1059–1062.
- Lentz, D.L., ed. (2000) *Imperfect balance: landscape transformations in the Precolumbian Americas*. Columbia University Press, New York.
- Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impact of exotic plant invasions in terrestrial ecosystems. *Proceedings of the Royal Society of London, Series B*, **270**, 775–781.
- Lugo, A.E. (2004) The outcome of alien tree invasions in Puerto Rico. *Frontiers of Ecology and the Environment*, **2**, 265–273.
- McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, **14**, 450–453.
- McNeely, J.A. (2000) The future of alien invasive species: changing social views. *Invasive species in a changing world* (ed. by H.A. Mooney and R.J. Hobbs), pp. 171–190. Island Press, Washington, DC.
- Meinesz, A. (1999) *Killer algae: the true tale of a biology invasion* (translated by D. Simberloff). University of Chicago Press, Chicago.
- Menge, B.A. & Sutherland, J.P. (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist*, **130**, 730–757.
- Milton, S.J. (2003) 'Emerging ecosystems': a washing-stone for ecologists, economists and sociologists? *South African Journal of Science*, **99**, 404–406.
- Odum, H.T. (1962) Ecological tools and their use. Man and the ecosystem. *Proceedings of the Lockwood conference on the suburban forest and ecology* (ed. by P.E. Waggoner and J.D. Ovington), pp. 57–75. The Connecticut Agricultural Experiment Station, Bulletin 652.
- Olden, J.D., LeRoy Poff, N., Douglas, M.R., Douglas, M.E. & Fausch, K.D. (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, **19**, 18–23.
- Peñuelas, J., Filella, I. & Comas, P. (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology*, **8**, 531–544.
- Postel, S.L., Morrison, J.I. & Gleick, P.H. (1998) Allocating fresh water to aquatic ecosystems: the case of the Colorado River Delta. *Water International*, **23**, 119–125.
- Redford, K.H. & Richter, B.D. (1999) Conservation of biodiversity in a world of use. *Conservation Biology*, **13**, 1246–1256.
- Redman, C.L. (1999) *Human impact on ancient environments*. University of Arizona Press, Tucson.
- Richardson, D.M. & Cowling, R.M. (1992) Why is mountain fynbos invulnerable and which species invade? *Fire in South African mountain fynbos: ecosystem, community and species response at Swartboskloof* (ed. by B.W. van Wilgen, D.M. Richardson, F.J. Kruger and H.J. van Hensbergen), pp. 161–181. Springer-Verlag, Berlin.
- Richardson, D.M., van Wilgen, B.W., Higgins, S.I., Trinder-Smith, T.H., Cowling, R.M. & McKell, D.H. (1996) Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. *Biodiversity and Conservation*, **5**, 607–647.
- Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. & Woolmer, G. (2002) The human footprint and the last of the wild. *Bioscience*, **52**, 891–904.
- Sauer, J.D. (1988) *Plant migration: the dynamics of geographic patterning in seed plant species*. University of California Press, Berkeley and Los Angeles.
- Scott, D.F. & Lesch, W. (1996) The effects of riparian clearing and clearfelling of an indigenous forest on streamflow, stormflow and water quality. *South African Forestry Journal*, **175**, 1–14.
- Simenstad, C.A., Estes, J.A. & Kenyon, K.W. (1987) Aleuts, sea otters, and alternative stable-state communities. *Science*, **200**, 403–410.
- Treskonova, M. (1991) Changes in the structure of tall tussock grasslands and infestation by species of *Hieracium* in the Mackenzie country, New Zealand. *New Zealand Journal of Ecology*, **15**, 65–78.

- Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M. & Westbrooks, R. (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology*, **21**, 1–16.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.
- Ward, J.V. & Stanford, J.A. (1979) *The ecology of regulated streams*. Plenum Press, New York.
- Whisenant, S.G. (1999) *Repairing damaged wildlands: a process-orientated, landscape-scale approach*. Cambridge University Press, Cambridge.
- Wilkinson, D.M. (2004) The parable of Green Mountain: Ascension Island, ecosystem construction and ecological fitting. *Journal of Biogeography*, **31**, 1–4.
- Zavaleta, E.S., Hobbs, R.J. & Mooney, H.A. (2001) Maximizing the benefits of eradication: why invasive species removal

should be viewed in a whole-ecosystem context. *Trends in Ecology and Evolution*, **16**, 454–459.

- Zimmerman, J.K., Pascarella, J.B. & Aide, T.M. (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology*, **8**, 350–360.

BIOSKETCH

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Editor: Tim Blackburn