

been made to MSB is that an increase in variance has not been seen in selection experiments [4]. Such arguments ignore, however, correlations of gene frequency change that are produced by the selection and check the increase in variance. In simulations, samples in MSB under the joint model were subjected to artificial selection [14]. The results were broadly similar to those from experiments [1]. Directional selection experiments are not, however, very discriminatory; for example, the infinitesimal model of many unlinked additive genes each of infinitesimally small effect also fits quite well.

### Conclusions

Mutation–selection balance is, therefore, a plausible and indeed probable mechanism whereby quantitative genetic variation is maintained in populations for traits under stabilizing selection. The recent analysis suggests that most of the variation maintained in the quantitative trait is contributed by genes that are nearly neutral for fitness in heterozygotes, and that most of the observed stabilizing selection is contributed by genes that have large effects on the trait [5,9]. There are, however, many simplifications in the model; for example, it includes no epistasis or genotype  $\times$  environment interaction. This is not to say that such factors are not important, but that they are not necessary. In view of the ubiquitous nature of genetic variation, it is important to seek mechanisms that are universal, and the fewer parameters required to do so, the better.

### Acknowledgements

This work was supported by a grant from the Biotechnology and Biological Sciences Research Council, UK.

### References

1 Falconer, D.S. and Mackay, T.F.C. (1996) *Introduction to Quantitative Genetics*, (4th edn), Longman

- 2 Endler, J.A. (1986) *Natural Selection in the Wild*, Princeton University Press
- 3 Lynch, M. and Walsh, B. (1998) *Genetics and Analysis of Quantitative Traits*, Sinauer
- 4 Maynard Smith, J. (1989) *Evolutionary Genetics*, Oxford University Press
- 5 Zhang, X.S. *et al.* (2004) Influence of dominance, leptokurtosis and pleiotropy of deleterious mutations on quantitative genetic variance at mutation–selection balance. *Genetics* 166, 597–610
- 6 Kimura, M. (1965) A stochastic model concerning the maintenance of genetic variability in quantitative characters. *Proc. Natl. Acad. Sci. U. S. A.* 54, 731–736
- 7 Turelli, M. (1984) Heritable genetic variation via mutation–selection balance: Lerch's Zeta meets the abdominal bristle. *Theor. Popul. Biol.* 25, 138–193
- 8 Robertson, A. (1967) The nature of quantitative genetic variation. In *Heritage from Mendel* (Brink, A., ed.), pp. 265–280, University of Wisconsin Press
- 9 Barton, N.H. (1990) Pleiotropic models of quantitative variation. *Genetics* 124, 773–782
- 10 Keightley, P.D. and Hill, W.G. (1990) Variation maintained in quantitative traits with mutation–selection balance: pleiotropic side-effects on fitness traits. *Proc. R. Soc. Lond. B Biol. Sci.* 242, 95–100
- 11 Kondrashov, A.S. and Turelli, M. (1992) Deleterious mutations, apparent stabilizing selection and the maintenance of quantitative variation. *Genetics* 132, 603–618
- 12 Caballero, A. and Keightley, P.D. (1994) A pleiotropic nonadditive model of variation in quantitative traits. *Genetics* 138, 883–900
- 13 Zhang, X.S. *et al.* (2004) Redistribution of gene frequency and changes of genetic variation following a bottleneck in population size. *Genetics* 167, 1475–1492
- 14 Zhang, X.S. and Hill, W.G. (2005) Predictions of patterns of response to artificial selection in lines derived from natural populations. *Genetics* 169, 411–425
- 15 García-Dorado, A. *et al.* (2004) Rates and effects of deleterious mutations and their evolutionary consequences. In *Evolution of Molecules and Ecosystems* (Moya, A. and Font, E., eds), pp. 20–32, Oxford University Press

0169-5347/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.  
doi:10.1016/j.tree.2005.06.010

## Are invasive species the drivers of ecological change?

Raphael K. Didham<sup>1</sup>, Jason M. Tylianakis<sup>2</sup>, Melissa A. Hutchison<sup>1</sup>, Robert M. Ewers<sup>3</sup> and Neil J. Gemmill<sup>1</sup>

<sup>1</sup>School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

<sup>2</sup>Fachgebiet Agrarökologie, Georg August Universität, Waldweg 26, Göttingen, D-37073, Germany

<sup>3</sup>Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panama, Republic of Panama

**Invasive species are widely accepted as one of the leading direct causes of biodiversity loss. However, much of the evidence for this contention is based on simple correlations between exotic dominance and native species decline in degraded systems. Although appealing, direct causality is not the only possible interpretation. A plausible alternative hypothesis is that exotic dominance could be the indirect**

**consequence of habitat modification driving native species loss. In a new paper, MacDougall and Turkington now provide the first direct test of whether invasive species are the drivers of community change, or merely 'passengers' along for the environmental ride.**

### The Homogocene

Almost 20 years after Gordon Orians popularized the dawning of the 'Homogocene' era [1], the term has become

Corresponding author: Didham, R.K. (raphael.didham@canterbury.ac.nz).

Available online 21 July 2005

evocative of an unprecedented global redistribution of species. Non-native species now dominate most landscapes in most parts of the world, owing to the propagation of 'beneficial' species and the inadvertent spread of 'pest' species by humans. However, as recently as 1996, Peter Vitousek and colleagues considered that even the ecologists and conservation biologists working to control pest invasions were not taking the problem seriously enough, and called for wider recognition of the global consequences of invasions for the loss of biodiversity [2]. There has since been a significant increase in the emphasis placed on invasive species as one of the leading causes of species decline [3], and biological invasion is now considered to be one of the 'big five' environmental issues of public concern [4]. Media attention has engendered considerable hyperbole about the global impacts of invasive species [5], but there is a growing disquiet among ecologists that the scientific literature has also become rife with uncritical generalizations [1,6,7].

A recent Opinion article in *TREE* [7] focuses the scientific issues more clearly and questions whether there is strong evidence for invasive species as a direct cause of native species decline [8,9]. Of central importance is whether the ubiquitous positive correlation between native species decline and invasive species dominance necessarily means that invasive species are the drivers of the observed change. Many invasive species take opportunistic advantage of other forms of ecosystem change, such as habitat disturbance, rather than being the drivers of change themselves [7]. In itself, this observation is nothing new, and similar statements have been echoed in every major review of invasive species impacts in the past ten years (e.g. [2,10,11]). What is important is recognizing that, if we are to better understand the impacts of invasive species and mitigate threats to native species, we must be able to distinguish between different causal mechanisms of population decline. Strong correlations with putative drivers are no substitute for mechanistic discrimination among factors [7].

Unfortunately, research on the two major recognized drivers of species decline, habitat loss and species invasions, is often approached as though they are independent single-factor problems, rather than factors that interact additively or synergistically [12,13]. When multiple causal agents of decline are considered, it is usually in a qualitative or conditional sense, rather than in quantitative analyses [13]. Furthermore, even the few invasion studies that do take a mechanistic experimental approach [14] typically have a singular invasion focus, rather than first testing the causal linkages between invasion and habitat disturbance (Box 1). In this context, a new paper by MacDougall and Turkington [15] brings a decisive and much-needed hypothesis-testing approach to evaluating whether invasive species are the cause of widespread ecological change, or simply a correlate of habitat disturbance by humans.

### **Invasive species: drivers or passengers of ecological change?**

The garry oak *Quercus garryana* meadows of southwest Canada and northwest USA are a good system in which to

tease apart the relative impacts of habitat disturbance and invasion on native species decline [15]. Species invasion has been severe, with 144 naturalized exotic plant species (32% of the regional flora) representing 55–75% of local species richness and 80–90% of biomass [15,16]. The overwhelming impression is that native species have all but been displaced by invasive species, with the inference being that the invaders are competitively dominant over resident natives. However, anthropogenic habitat alteration covaries strongly with invasion impacts [15,16], with only 1–5% of original habitat remaining and a history of long-term fire suppression [16]. Consequently, exotic dominance could have less to do with strong species interactions, such as competitive displacement, than with non-interactive processes, such as relative dispersal ability or altered disturbance regimes that are more limiting for native species than they are for invasive species [15,17,18].

The experimental approach taken to test between these contrasting hypotheses was straightforward [15]. MacDougall and Turkington reasoned that, if interactive processes are responsible for native species decline, then removal of invasive species should result in a direct increase in the richness and relative abundance of native species (the 'driver' model) (Box 2, Figure 1a). Conversely, if invasive species are not the limiting factor for native species, then eradication should have minimal impact (the 'passenger' model) (Box 2, Figure 1b).

MacDougall and Turkington established a factorial field experiment examining the impact of biomass reduction (mowing) and complete removal (weeding) of the two dominant exotic grasses, *Poa pratensis* and *Dactylis glomerata* (comprising ca. 50–80% total cover), on native plant richness and relative abundance. After three years of treatment imposition, both treatments caused a rapid and persistent decrease in total production and a gradual shift in dominance from perennial grasses to perennial forbs. Most of the compensation was by native forbs already established before experimental treatments, and there was little recruitment of either native or exotic perennial species into plots within three years [15]. In fact, almost half of the resident species showed no change or decreased significantly in percent cover following exotic dominant removal. The recovery of native species dominance predicted by the driver model following invasive species removal did not occur (Box 2, Figure 1a), and the data suggest that the passenger model is the underlying cause of exotic dominance in this system (Box 2, Figure 1b).

Under the passenger model, non-interactive processes, such as inferior dispersal ability and sensitivity to habitat disturbance, are hypothesized to limit native species. The field experiment showed that natural recruitment of native species was negligible over a three-year period. However, to distinguish between recruitment limitation and germination success, a seed addition experiment was performed that showed that native seedling survival (although low) was possible even under heavy exotic cover in control plots, and that survival was significantly enhanced by exotic dominant removal [15]. Similar results

### Box 1. Chains of causality

In systems with multiple stressors, not only is it difficult to discriminate between the causes and correlates of population decline, but it is also equally difficult to determine the relative importance of different causal mechanisms. Whereas the direct impacts of individual drivers can be readily recognized, indirect causal linkages among multiple drivers can be complex to detect and quantify. For example, habitat disturbance frequently increases the impacts of invasive species [11], which can themselves alter disturbance regimes [23], and both can have strong indirect effects on native populations. What then is the 'cause' of population decline in these situations? And how much more complex is the answer likely to be if there are more than two interacting drivers? Here, we restrict many of our arguments to habitat disturbance and invasion for the sake of simplicity, but these are just two of many possible causal agents of decline. Vitousek and colleagues [2,25] make a compelling case that these individual cause and effect relationships are embedded within a larger cascading series of linkages that ultimately stem from the vast scale of human enterprise (Figure 1).

In a mechanistic sense, it is not particularly helpful to resort to increased human population pressure as the root cause of all local population declines. However, drawing a distinction between the

proximate versus ultimate causes of population decline, and between the factors that directly or indirectly limit population recovery [26] will greatly increase our ability to manage threatened species more effectively [7,27]. For example, in the debate over the importance of zebra mussels *Dreissena polymorpha* as a causal agent of unionid mussel extinctions in the USA [7,8,27], Gurevitch and Padilla [27] note that population declines and extinctions were widespread before zebra mussel invasion, and they question whether the invaders would have had the same impact if unionid populations had not already been greatly reduced by decades of habitat disturbance, over-harvesting and water pollution. In principle, this problem is potentially even more insidious and difficult to detect than are other chains of causality because the synergies might not necessarily result from contemporary interactions among factors. Historical processes might drive populations to low levels and then halt or dissipate, whereas the resulting small population becomes vulnerable to a different or additional set of factors. Pragmatically, these issues matter for conservation managers because focusing attention on the direct, proximate agent perceived to be limiting population recovery might not necessarily result in long-term success.

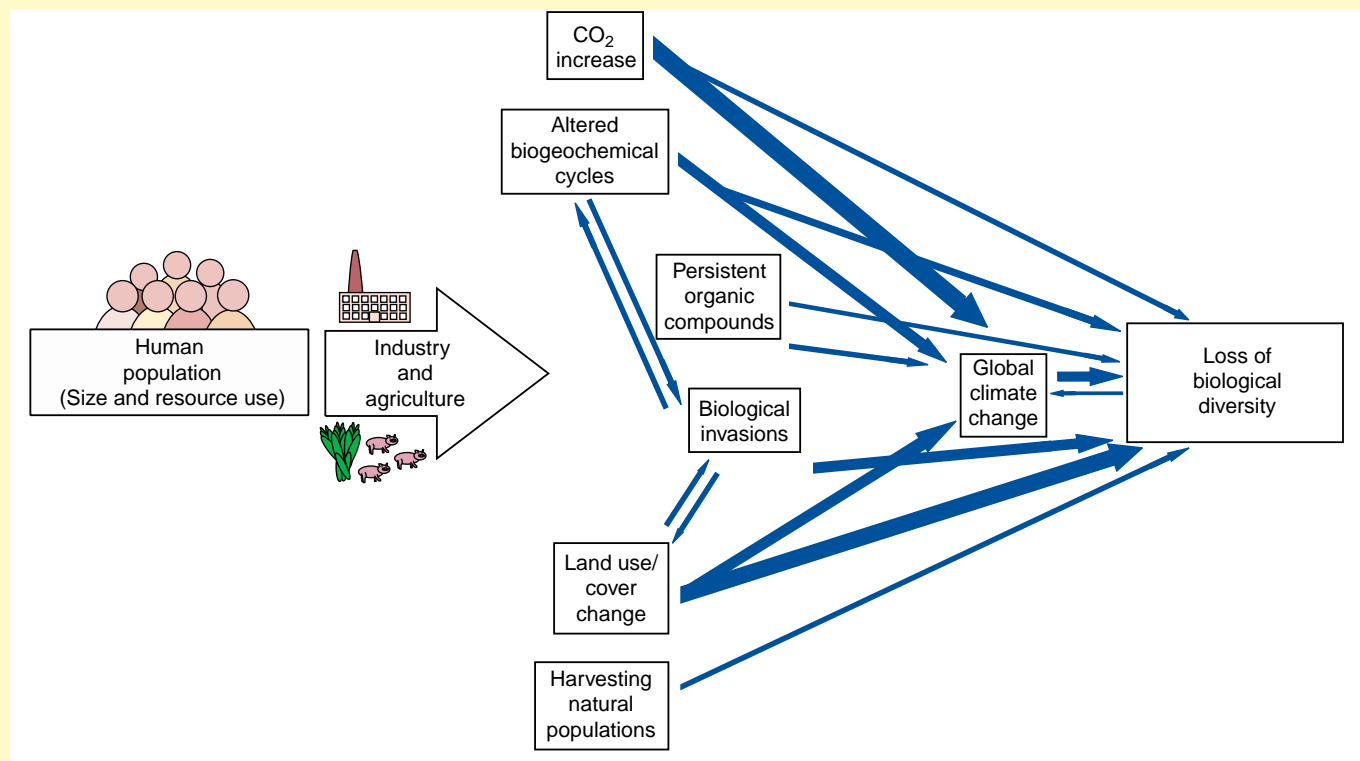


Figure 1. Interactions among multiple drivers of biodiversity loss. Modified with permission from [2,25].

from previous studies [18–20] suggest that recruitment limitation of native species is a more widespread explanation for exotic dominance in degraded systems than is competitive exclusion.

### Additive or synergistic effects of habitat disturbance and species invasions

Invasive species can have significant effects on resource availability and can suppress or enhance the relative abundance of native species, without necessarily being the driving force behind community change. In spite of general support for the passenger model, there was evidence that some native species increased significantly

in percent cover or productivity following removal of exotic dominants (Box 2, Figure 1c). This implies that the sequestration of light, space and nutrients by *P. pratensis* and *D. glomerata* did limit growth for these species. If we interpret this as some form of cause and effect relationship (whether direct or indirect; Box 1), then it points more toward an 'interacting drivers' explanation than a strict interpretation of the passenger model would suggest. It is probably more realistic to consider the driver and passenger models as extreme cases of a general model incorporating additive or synergistic effects of the two factors (Box 2, Figure 1c), with the relative importance of invasive species and habitat disturbance varying between

### Box 2. Models describing the drivers of ecological change in degraded systems

In the driver model (Figure 1a), there are strong biotic interactions between exotic invaders and native residents (indicated by double-headed arrows), and exotic dominance in contemporary landscapes is a direct consequence of competitive exclusion of native species. The model predicts that experimental removal of dominant exotic species should result in native species recovery. In the passenger model (Figure 1b), habitat disturbance has direct negative effects on native species, but biotic interactions between invasive and native species are weak or non-existent, and exotic dominance occurs by invaders 'filling the void'. The driver and passenger models are limiting cases of a more general model with additive or synergistic effects among multiple causal agents of decline (Figure 1c). For simplicity, only the two major causal agents, habitat disturbance and invasion, are shown (Box 1) and we give them equal importance in determining exotic dominance, although their effects are more likely to be unequal. In a few cases, a positive feedback loop between habitat disturbance and species invasion has been implicated in the 'invasional meltdown' of disturbed ecosystems [28]. In all cases, the contemporary landscapes

are dominated 90:10 by exotics and it is impossible to distinguish which model is operating simply by observation alone. Following invasive species removal, the interacting drivers model predicts that there will be partial recovery of some native species (e.g. Sp. A, sp. B), but not others (e.g. sp. C). Experimental data point towards the passenger model as the underlying cause of exotic dominance [15].

Data in Figure 1b are redrawn with permission from [15] and depict summer weeding treatments to remove the dominant exotic species *Poa pratensis* and *Dactylis glomerata* in deep-soil plots. The non-significant trends are representative of other treatment effects. However, MacDougall and Turkington note that the combined suppressive and facilitative effects of habitat disturbance and species invasion are substantial and that some native species did benefit from exotic species removal. Data in Figure 1c are redrawn with permission from [15] for the native forb *Camassia quamash* and depict summer weeding treatments in shallow soil plots. Trends are not representative of other species or treatment responses.

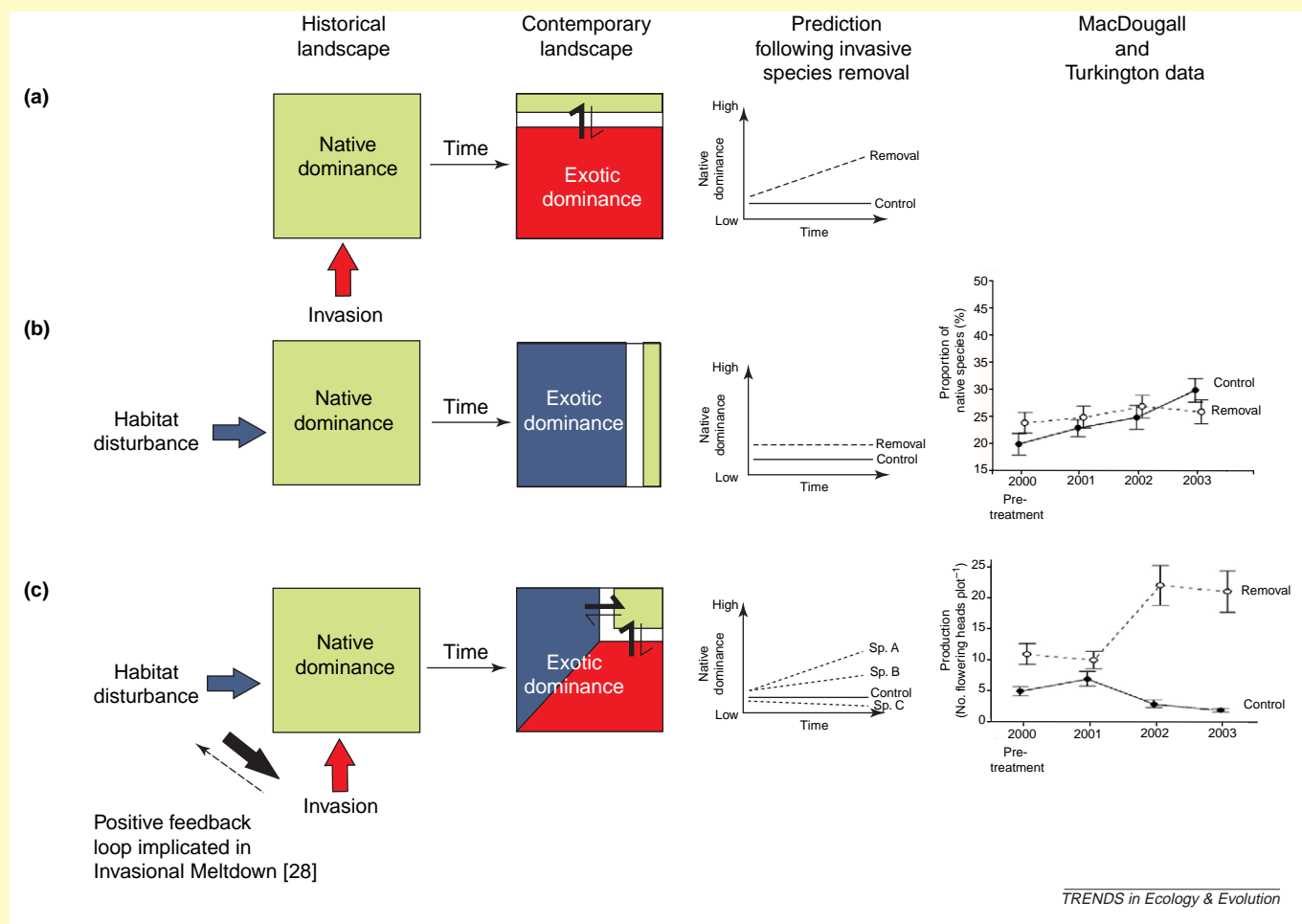


Figure 1.

species and between ecosystems. For example, in Hawai'i, Petren and Case [21] found experimental evidence that direct exploitation competition by the invasive gecko *Hemidactylus frenatus* caused population decline in the native gecko *Lepidodactylus lugubris*, but only in the context of altered resource distributions (increased clumping of insect prey) that occurred following anthropogenic habitat disturbance.

MacDougall and Turkington make the interesting observation that there are also positive impacts of exotic dominant grasses in garry oak meadows. Most importantly, *P. pratensis* and *D. glomerata* dominance appears to maintain the open savannah structure that is so characteristic of garry oak ecosystems by inhibiting succession to exotic woodland. Of course, this same role would probably be performed by functionally equivalent

native perennial grasses if they were not so dispersal limited relative to the exotic dominants. Nevertheless, dominance by exotic perennial grasses does appear to be the lesser of the two evils. Furthermore, *P. pratensis* and *D. glomerata* might also act as 'nursery plants', which enhance the survival of native seedlings if aboveground exotic biomass is reduced by mowing in autumn. In combination with the overall conclusion that native seed supply is limiting ecosystem recovery, these results present obvious management prescriptions for restoring native dominance in garry oak meadows.

### Limitations on a small-scale experimental approach

There are several limitations on experimental demonstration of invasive species impacts. First, not all invasive species, or invaded ecosystems, are amenable to experimental manipulation. Although manipulative experiments can typically provide greater mechanistic understanding of the drivers of ecological change, judicious use of comparative quantitative data can also be powerful in testing the degree of intercorrelation among multiple drivers. For example, Farnsworth [22] found that the decline of rare native plants across New England, USA, was determined by the same habitat disturbance and site management variables that were associated with invasive species presence, rather than by the presence of invasive species alone.

Second, even when systems can be manipulated, an inherent limitation of any small-scale experiment is the inability to detect the historical drivers of ecological change in situations where the system has been irreversibly altered (Box 1). For example, invasive species might alter disturbance regimes [23] and cause an ecosystem to shift to an alternative stable state, yet it might not be possible to detect this driving role because invasive species removal does not result in ecosystem recovery. Third, when three or more drivers of ecological change are acting in concert, the direct and indirect linkages among factors might be too complex to test experimentally. In all of these cases, discriminating among potential drivers of species decline will require a combination of approaches incorporating quantitative empirical data, experimentation and structural equation modelling, such as path analysis [24].

### Prospects

Although the generality of the passenger model as an explanation for exotic dominance in degraded systems is highly contentious in its own right, in many respects it is not the overall conclusions of MacDougall and Turkington that are the most important contribution of their paper. After all, the ultimate causes of population decline are species specific and context dependent, and there will be other systems in which the driver model is more applicable. Instead, the real value of their paper lies in the fact that they raised testable hypotheses to discriminate among different explanatory models in the first place. Their study highlights the need for a greater awareness of the interactions among multiple drivers of species loss and greater scientific rigour in assessing the mechanistic causes of population decline.

### Acknowledgements

We thank Nicholas Gotelli, Jessica Gurevitch, Andrew MacDougall and an anonymous reviewer for helpful comments on the article.

### References

- Rosenzweig, M.L. (2001) The four questions: what does the introduction of exotic species do to diversity? *Evol. Ecol. Res.* 3, 361–367
- Vitousek, P.M. *et al.* (1996) Biological invasions as global environmental change. *Am. Sci.* 84, 468–478
- Wilcove, D.S. *et al.* (1998) Quantifying threats to imperiled species in the United States. *Bioscience* 48, 607–615
- Sala, O.E. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774
- Simberloff, D. (2004) Review of "Invasion biology: critique of a pseudoscience". *Ecol. Econ.* 48, 360–362
- Slobodkin, L.B. (2001) The good, the bad and the reified. *Evol. Ecol. Res.* 3, 1–13
- Gurevitch, J. and Padilla, D.K. (2004) Are invasive species a major cause of extinctions? *Trends Ecol. Evol.* 19, 470–474
- Ricciardi, A. (2004) Assessing species invasions as a cause of extinction. *Trends Ecol. Evol.* 19, 619
- Clavero, M. and Garcia-Berthou, E. (2005) Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol.* 20, 110
- Mack, R.N. *et al.* (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10, 689–710
- Byers, J.E. (2002) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97, 449–458
- Fazey, I. *et al.* (2005) What do conservation biologists publish? *Biol. Conserv.* 124, 63–73
- Didham, R.K. *et al.* (2005) Comment on "Avian extinction and mammalian introductions on oceanic islands". *Science* 307, 1412a
- Parker, I.M. *et al.* (1999) Impact: towards a framework for understanding the ecological effects of invaders. *Biol. Inv.* 1, 3–19
- MacDougall, A.S. and Turkington, R. (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86, 42–55
- MacDougall, A.S. *et al.* (2004) Defining conservation strategies with historical perspectives: a case study from a degraded oak grassland ecosystem. *Conserv. Biol.* 18, 455–465
- Davis, M.A. (2003) Biotic globalization: does competition from introduced species threaten biodiversity? *Bioscience* 53, 481–489
- Seabloom, E.W. *et al.* (2003) Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl. Acad. Sci. U. S. A.* 100, 13384–13389
- Foster, B.L. and Tilman, D. (2003) Seed limitation and the regulation of community structure in oak savanna grassland. *J. Ecol.* 91, 999–1007
- Corbin, J.D. and D'Antonio, C.M. (2004) Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology* 85, 1273–1283
- Petren, K. and Case, T.J. (1996) An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* 77, 118–132
- Farnsworth, E.J. (2004) Patterns of plant invasions at sites with rare plant species throughout New England. *Rhodora* 106, 97–117
- Mack, M.C. and D'Antonio, C.M. (1998) Impacts of biological invasions on disturbance regimes. *Trends Ecol. Evol.* 13, 195–198
- Wootton, J.T. (1994) Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75, 151–165
- Vitousek, P.M. *et al.* (1997) Human domination of Earth's ecosystems. *Science* 277, 494–499
- Caughley, G. (1994) Directions in conservation biology. *J. Anim. Ecol.* 63, 215–244
- Gurevitch, J. and Padilla, D.K. (2004) Response to Ricciardi: Assessing species invasions as a cause of extinction. *Trends Ecol. Evol.* 19, 620
- Simberloff, D. and von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biol. Inv.* 1, 21–32