

Misleading criticisms of invasion science: a field guide

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INTRODUCTION

Invasion science is the study of the causes and consequences of the introduction of organisms to the areas outside their native ranges. It concerns all aspects relating to the transport, establishment and spread of organisms in a new target region, their interactions with resident organisms, and the costs and benefits of invasion with reference to human value systems. ‘Invasion science’ is a more appropriate name for the broad domain than ‘invasion ecology’ or ‘invasion biology’ because of the importance of engaging with many disciplines other than biology and ecology in understanding and managing invasions (Richardson *et al.*, 2011).

The scientific study of invasions has become increasingly popular, as indicated by the explosive growth of publications and academic books on the topic over the past two decades (Simberloff, 2004; Richardson & Pyšek, 2008). Aspects of invasion science now feature in virtually all textbooks and synthetic monographs of ecology, conservation biology, biogeography and evolution. Another metric of the burgeoning impact of research on invasions is its coverage in the most highly cited journals in many disciplines: Figure 1 shows this for ecology over the past 15 years. Clearly, there has been a growing recognition that research on invasions is invaluable for understanding how most ecosystems work. Studies of invasions have yielded novel insights on key ecological concepts, including *inter alia* the diversity–stability relationship, trophic cascades, keystone species, the role of disturbance in community assembly, ecological naïveté, ecological fitting, rapid evolution, island biogeography, ecosystem engineering and niche construction. The field has also contributed concepts of its own (e.g. propagule pressure, biotic resistance, invasional meltdown, enemy release) that have stimulated productive research of both theoretical and applied importance.

A key motivation for studying invasions is their environmental impact. Non-native species are far more likely to have ecological and socio-economic impacts than do those native species that, for various reasons, undergo range expansions or increase in abundance to become ‘weedy’ (Simberloff *et al.*, 2012). The negative impacts of non-native consumers are far greater than those of native consumers (e.g. Paolucci *et al.*, 2013). Numerous studies demonstrate the role of invasions as a driver of species loss at local and regional scales (e.g. Wyatt *et al.*, 2008; Burghardt *et al.*, 2010; Baider & Florens, 2011; Roy *et al.*, 2012; Gilbert & Levine, 2013), even where other confounding stressors are at play (e.g. Light &

Marchetti, 2007; Hermoso *et al.*, 2011). Evidence points to non-native species as a major cause of global animal extinctions (Clavero & García-Berthou, 2005; Clavero *et al.*, 2009). They also raise the extinction likelihood of native plant populations; the substantial time-lags inherent in these population extinctions are frequently ignored, resulting in spurious conclusions on the magnitude of invasions as eroders of plant biodiversity (Gilbert & Levine, 2013). Non-native species are frequently implicated as components of a lethal cocktail of stressors on biodiversity (van der Wal *et al.*, 2008; Schweiger *et al.*, 2010; Blaustein *et al.*, 2011). Even where other stressors have already diminished native populations, invasions can accelerate these declines (e.g. Ricciardi, 2004). Finally, invasions also disrupt key ecological processes. Many such disruptions are subtle (e.g. Stinson *et al.*, 2006) and may take decades to unfold or for their implications to manifest, as in the case of plant–animal mutualisms (Traveset & Richardson, 2006; Davis *et al.*, 2010; Sekercioglu, 2011).

The societal importance of biological invasions is illustrated by the growing socio-economic costs of invasions to agriculture, forestry, aquaculture, apiculture, technological (e.g. water supply) systems and human health, as well as potentially myriad positive and negative effects on ecosystem services (Cook *et al.*, 2007; Pejchar & Mooney, 2009; Pyšek & Richardson, 2010; Rothlisberger *et al.*, 2012). Thus, it is not surprising that invasions are increasingly viewed as an issue of national security (e.g. Penman, 1998; Meyerson & Reaser, 2003; Chomel & Sun, 2010; Ricciardi *et al.*, 2011).

A cottage industry of criticisms

Despite the accumulation of rigorous evidence of its importance to science and society, invasion science has been the target of criticisms from a relatively small but vocal number of scientists and academics – naysayers in various guises. Challenges to the concepts, philosophical underpinnings and methods of young growing disciplines are necessary to force practitioners to sharpen their science (e.g. Richardson, 2009). However, many of the criticisms against invasion science simply do not withstand scrutiny. These criticisms may be grouped into six broad non-exclusive categories (Table 1). Some critics raise issues with particular notions or assumptions relating to research agendas in the field, some dispute links between results of studies and implications for management, whereas others go so far as to question the need for the field, or its long-term viability, and call for ‘participants [to] consider abolishing their discipline’ (Davis, 2009;

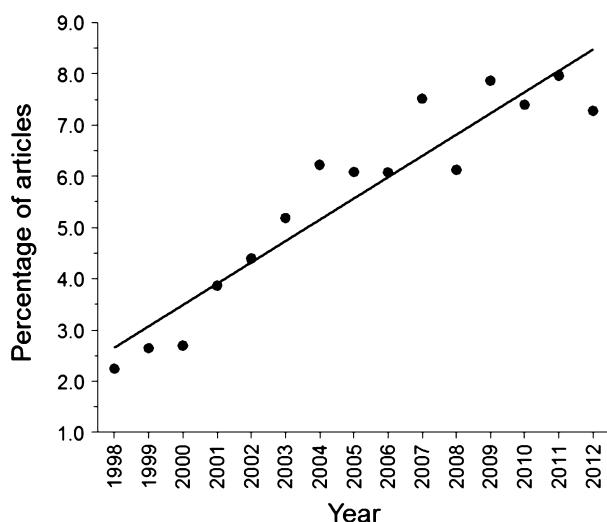


Figure 1 The increasing proportional contribution of articles dealing with biological invasions in five general ecology journals ranked among the highest in their field in terms of impact factor (*Ecology Letters*; *Trends in Ecology and Evolution*; *Annual Reviews in Ecology, Evolution, and Systematics*; *Ecological Monographs*; *Ecology*). Articles published from 1998 to 2012 were located using Web of Science and the following search string: ‘biological invasion’ OR ‘species invasion’ OR ‘species introduction’ OR invasive OR non-native OR non-indigenous OR alien OR ‘exotic species’ OR ‘introduced species’ OR ‘invasion ecology’ OR ‘invasion biology’. The line was fitted by least-squares regression: $R^2 = 0.88$, $P < 0.0001$.

p. 191) or ‘the end of invasion biology’ (Valéry *et al.*, 2013). Another major criticism is that most invasions are benign and thus do not merit management, such as the oft-repeated claim that management efforts are being wasted on innocuous non-native species – activities described as ‘irrational’ and ‘deliberate persecution’ (Thomas, 2013). In reality, managers are constrained by limited resources and seek to prioritize species that are likely to become problematic. However, this effort is hampered by several facts that are generally ignored by the naysayers: (1) the impacts of most invasions have not been studied, and so important effects may remain undetected, (2) invaders that are apparently innocuous in one region can be disruptive in other regions, (3) subtle impacts that may be unrecognizable without careful technical study can produce enormous ecosystem changes over time, and (4) many non-native species that currently appear innocuous may become damaging many years later – when it is no longer feasible to eradicate them (van der Wal *et al.*, 2008; Simberloff, 2011; Ricciardi *et al.*, 2013; Simberloff *et al.*, 2013).

Another claim is that the biogeographic origins of a species are irrelevant to its impact and thus should have no bearing on its management (Davis *et al.*, 2011). In a similar vein, critics claim that the native/non-native dichotomy (and thus the entire field) holds no scientific value (Davis *et al.*, 2011; Thompson & Davis, 2011; Valéry *et al.*, 2013). These claims are countered by research that has demonstrated the

importance of evolutionary history in the outcome of invasions. Such research helps explain why non-native consumers inflict greater damage on native populations (Salo *et al.*, 2007; Paolucci *et al.*, 2013), why there is a greater incidence of pest species among non-native versus native plants (Simberloff *et al.*, 2012), why some invaders have stronger impacts in their non-native ranges than in their native ranges (Callaway *et al.*, 2012) and why the introduction of phylogenetically novel species are more likely to cause ecological disruptions (Short *et al.*, 2002; Ricciardi & Atkinson, 2004; Strauss *et al.*, 2006). Clearly, the biogeographic origins of species *do* matter to understanding why some invasions cause greater impacts than others.

Reformulations of the arguments summarized in Table 1 continue to be published, even after being challenged or refuted. In our view, the escalation of cavalier bashing of the discipline is undermining systematic science-based efforts to improve the efficiency of management of problematic non-native species and invaded ecosystems (Lambertini *et al.*, 2011).

Premature obituaries: in search of causes

Why the upsurge in ‘obituaries’ for invasion ecology/science? Perhaps reflecting on the phenomenon of false or premature obituaries for humans may shed some light in this regard. An entry on ‘premature obituaries’ in Wikipedia (http://en.wikipedia.org/wiki/List_of_premature_obituaries; accessed 15 September 2013) details an impressive list of people whose death was chronicled while they were still alive. The article lists some general causes of the phenomenon and ascribes the false records of demise of most of the people mentioned to one of the following reasons: ‘accidental publication’; ‘brush with death’; ‘fraud victim’; ‘hoax’; ‘impostor’; ‘misidentified body’; ‘missing in action’; ‘misunderstandings’; ‘name confusion’; and ‘pseudocide’ (for elucidation of these categories, see the Wikipedia article).

Do any of these causes of false/premature obituaries for humans help to explain the upsurge in obituaries and death wishes for invasion science? Several can be discarded; it is difficult to see how ‘accidental publication’, ‘fraud victim’, ‘hoax’, ‘impostor’, ‘missing in action’ or ‘pseudocide’ could elucidate the necrologies for the field. ‘Brush with death’ may have a role, as some detractors seem to think that invasion science is seriously ill and that it is only a matter of time before the field is abandoned (Davis & Thompson, 2002; Thompson & Davis, 2011; Valéry *et al.*, 2013). More compelling, however, are the remaining causes: ‘misidentified body’, ‘misunderstandings’ and ‘name confusion’. As one of us has argued previously, what many of the detractors write about is not invasion biology/ecology/science as understood and practised by almost all biogeographers, conservation biologists and ecologists (e.g. the definitions in Richardson *et al.* (2011) and the framework detailed in Blackburn *et al.*, 2011), but rather a caricature or parody of the discipline (Richardson *et al.*, 2008).

Table 1 A field guide to misleading criticisms of invasion science

Criticism	Sources	Rebuttal	Sources
1. <i>Modern invasions are nothing new.</i> The magnitude and impacts of human-assisted invasions are similar to those in the fossil record, that is, generally low, and thus do not merit major concern and concerted conservation action.	Brown & Sax (2004, 2005); Vermeij (2005); Briggs (2013)	The current scale, impact and evolutionary importance of invasions are unique. Under human influence, organisms are spreading faster, farther and in greater numbers than ever before. Human-mediated introductions create dispersal pathways that are fundamentally distinct from those possible for spread events not involving human actions. This facilitates colonization events that are inadequately explained by natural dispersal models.	Cassey <i>et al.</i> (2005); Ricciardi (2007); Wilson <i>et al.</i> (2009b)
2. <i>Impacts of non-native species on biodiversity and ecosystems are exaggerated.</i>	Rosenzweig (2001); Brown & Sax (2004, 2005); Sagoff (2005); Gurevitch & Padilla (2004); Goodenough (2010); Davis <i>et al.</i> (2011); Briggs (2013); Thomas (2013)	Global data sets clearly implicate invasions as a major and growing cause of population-level and species-level extinctions. Decades of experimental research have demonstrated the capacity for invasions to alter ecosystems. Impacts of invasions on plant extinction are frequently masked by the lengthy time-lags inherent in plant extinctions: numerous species affected by invasions survive as 'the living dead'.	Collins <i>et al.</i> (2002); Ricciardi (2004); Clavero & García-Berthou (2005); Simberloff (2005); Clavero <i>et al.</i> (2009); Simberloff (2011); Gilbert & Levine (2013)
3. <i>Increased species introductions raise biodiversity</i> (e.g. by adding to regional species pools; generating new taxa through hybridization) and therefore do not merit concern.	Brown & Sax (2004); Vermeij (2005); Thomas (2013)	Focusing on species richness counts ('the numbers game') is a misleading approach to quantifying impact, especially when the persistence of many species recorded over long time periods is not verified. Extinction may not be an appropriate measure of impact on ecosystem function. Assessment of the influence of invasions on the abundance and distribution of native species (and consequences of these changes on the functioning of ecosystems) is crucial. Hybridization has been shown to be a major contemporary extinction force, especially when accompanied by habitat homogenization, causing species declines through introgression, genetic swamping and reproductive interference.	Rhymer & Simberloff (1996); Ayres <i>et al.</i> (2004); Simberloff (2006); Jäger <i>et al.</i> (2009); Burghardt <i>et al.</i> (2010); Boero (2011)
4. <i>Positive (desirable) impacts of non-native species are understated and are at least as important as their negative (undesirable) impacts.</i>	Schlaepfer <i>et al.</i> (2011a, b)	Non-native species are far more likely to cause substantial ecological and socio-economic damage, such as ecosystem-level regime shifts, than are native species. Furthermore, many of the 'positive' impacts attributed to non-natives are likely to be transient, whereas the 'negative' impacts are typically more permanent and often irreversible.	Simberloff <i>et al.</i> (2012, 2013); Paolucci <i>et al.</i> (2013)
5. <i>Invasions science is biased and xenophobic.</i>	Warren (2007); Schlaepfer <i>et al.</i> (2011a, b)	Xenophobes obsessed with eradicating all non-native organisms operate on the fringe of the conservation movement – as do those who link informed efforts to manage introduced species with xenophobia.	Simberloff (2003); Richardson <i>et al.</i> (2008); Simberloff <i>et al.</i> (2011)
6. <i>The biogeographic origin of a species has no bearing on its impact. The native/non-native dichotomy holds no value to science.</i> Therefore, these factors should not guide management, and there is no rationale for invasion science.	Davis & Thompson (2002); Warren (2007); Davis (2011); Davis <i>et al.</i> (2011); Thompson & Davis (2011); Valéry <i>et al.</i> (2013)	Ignoring biogeographic origins as a mediator of impact ignores the importance of evolutionary context in species interactions. Non-native consumers inflict greater damage on native populations. The more 'alien' an established animal, plant or microbe is to its recipient community, the greater the likelihood it will be ecologically disruptive.	Ricciardi & Atkinson (2004); Strauss <i>et al.</i> (2006); Salo <i>et al.</i> (2007); Richardson <i>et al.</i> (2008); Wilson <i>et al.</i> (2009a); van Kleunen <i>et al.</i> (2011); Simberloff <i>et al.</i> (2012); Paolucci <i>et al.</i> (2013); Blondel <i>et al.</i> (in press)

A valuable and thriving metadiscipline

Contrary to its obituaries (and calls for its euthanizing), invasion science is a rapidly evolving interdisciplinary field that draws insights and perspectives from numerous other disciplines including epidemiology, immunology, palaeontology, macroeconomics, human geography and human history (Kueffer & Hirsch Hadorn, 2008; Richardson, 2011). Its growing impact on ecology (Fig. 1), for example, reflects a field that is thriving and becoming increasingly relevant, rather than one that is moribund. More and more, studies of invasions are incorporating sophisticated technologies such as molecular genetics methods, remote sensing and numerical modelling. In response to rapid global change, invasion ecologists are evaluating new concepts for understanding and managing biodiversity – including consideration of novel ecosystems (Richardson & Gaertner, 2013), managed relocation (Ricciardi & Simberloff, 2009), and methods of risk assessment for emerging threats (Leung *et al.*, 2012; Dick *et al.*, *in press*). It is well accepted that pragmatic approaches to dealing with non-native species are needed to ensure that limited resources are applied to the most important problems. Indeed, one of the principal goals of the field – to predict which introduced species will become disruptive – is of increasing societal importance, given the enormous rates of invasions driven by globalization (Ricciardi, 2007), the synergistic interactions of non-native species with one another and with multiple stressors including climate change (Schweiger *et al.*, 2010) and the potential flood of future novel organisms (e.g. GMOs, synthetic cells, products of nanotechnology) into the natural environment (Jeschke *et al.*, 2013). To suggest that non-native species are not unequivocally a major concern for the conservation of biodiversity and ecosystem services is to ignore decades of peer-reviewed science. Rather than write epitaphs or engage in arcane ideological debates, we need to move forward and continue to build on the knowledge we have gained. Although objective criticisms of the field are to be welcomed, there are many areas where received wisdom has been shown to be misleading. We would caution that the next author who feels they have convincingly killed off the field should check that they have not just remurdered a straw man.

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REFERENCES

- Ayres, D.R., Zaremba, K. & Strong, D.R. (2004) Extinction of a common native species by hybridization with an invasive congener. *Weed Technology*, **18**, 1288–1291.
- Baider, C. & Florens, F.B.V. (2011) Control of invasive alien weeds averts imminent plant extinction. *Biological Invasions*, **13**, 2641–2646.
- Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U. & Richardson, D.M. (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, **26**, 333–339.
- Blaustein, A.R., Han, B.A., Relyea, R.A., Johnson, P.T.J., Buck, J.C., Gervasi, S.S. & Kats, L.B. (2011) The complexity of amphibian population declines: understanding the role of cofactors in driving amphibian losses. *Annals of the New York Academy of Sciences*, **1223**, 108–119.
- Blondel, J., Hoffmann, B. & Courchamp, F. (*in press*) The end of Invasion Biology: intellectual debate does not equate to nonsensical science. *Biological Invasions*. DOI 10.1007/s10530-013-0560-6
- Boero, F. (2011) New species are welcome, but...what about the old ones? *Italian Journal of Zoology*, **78**, 1–2.
- Briggs, J.C. (2013) Invasion ecology: origin and biodiversity effects. *Environmental Skeptics and Critics*, **2**, 73–81.
- Brown, J.H. & Sax, D.F. (2004) An essay on some topics concerning invasive species. *Austral Ecology*, **29**, 530–536.
- Brown, J.H. & Sax, D.F. (2005) Biological invasions and scientific objectivity: reply to Cassey *et al.* (2005). *Austral Ecology*, **30**, 481–483.
- Burghardt, K., Tallamy, D.W., Philips, C. & Shropshire, K.J. (2010) Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere*, **1**, 1–22.
- Callaway, R.W., Schaffner, U., Thelen, G.C., Khamraev, A., Juginisorov, T. & Maron, J.L. (2012) Impact of *Acroptilon repens* on co-occurring native plants is greater in the invader's non-native range. *Biological Invasions*, **14**, 1143–1155.
- Cassey, P., Blackburn, T.M., Duncan, R.P. & Chown, S.L. (2005) Concerning invasive species: reply to Brown and Sax. *Austral Ecology*, **30**, 475–480.

- Chomel, B.B. & Sun, B. (2010) Bioterrorism and invasive species. *Revue Scientifique et Technique - Office International des Epizooties*, **29**, 193–199.
- Clavero, M. & García-Berthou, E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution*, **20**, 110.
- Clavero, M., Brotons, L., Pons, P. & Sol, D. (2009) Prominent role of invasive species in avian biodiversity loss. *Biological Conservation*, **142**, 2043–2049.
- Collins, M.D., Vázquez, D.P. & Sanders, N.J. (2002) Species-area curves, homogenization and the loss of global diversity. *Evolutionary Ecology Research*, **4**, 457–464.
- Cook, D.C., Tomas, M.B., Cunningham, S.A., Anderson, D.L. & De Barro, P.J. (2007) Predicting the economic impact of an invasive species on an ecosystem service. *Ecological Applications*, **17**, 1832–1840.
- Davis, M.A. (2009) *Invasion biology*. Oxford University Press, Oxford.
- Davis, M.A. (2011) Do native birds care whether their berries are native or exotic? No. *BioScience*, **61**, 501–502.
- Davis, M.A. & Thompson, K. (2002) “Newcomers” invade the field of invasion ecology: question the field’s future. *Bulletin of the Ecological Society of America*, **83**, 196–197.
- Davis, N.E., O’Dowd, D.J., MacNally, R. & Green, P.T. (2010) Invasive ants disrupt frugivory by endemic island birds. *Biology Letters*, **6**, 85–88.
- Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Del Tredici, P., Suding, K.N., Ehrenfeld, J.G., Grime, J.P., Mascaro, J. & Briggs, J.C. (2011) Don’t judge species on their origins. *Nature*, **474**, 153–154.
- Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B., Kumschick, S., Weyl, O.L.F., Dunn, A.M., Hatcher, M.J., Paterson, R.A., Farnsworth, K.D. & Richardson, D.M. (in press) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions*. DOI 10.1007/s10530-013-0550-8
- Gilbert, B. & Levine, J.M. (2013) Plant invasions and extinction debts. *Proceedings of the National Academy of Sciences USA*, **110**, 1744–1749.
- Goodenough, A. (2010) Are the ecological impacts of alien species misrepresented? A review of the “native good, alien bad” philosophy. *Community Ecology*, **11**, 13–21.
- Gurevitch, J. & Padilla, D.K. (2004) Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution*, **19**, 470–474.
- Hermoso, V., Clavero, M., Blanco-Garrido, F. & Prenda, J. (2011) Invasive species and habitat degradation in Iberian streams: an analysis of their role in freshwater fish diversity loss. *Ecological Applications*, **21**, 175–188.
- Jäger, H., Kowarik, I. & Tye, A. (2009) Destruction without extinction: long-term impacts of an invasive tree species on Galapagos highland vegetation. *Journal of Ecology*, **97**, 1252–1263.
- Jeschke, J.M., Keesing, F. & Ostfeld, R.S. (2013) Novel organisms: comparing invasive species, GMOs, and emerging pathogens. *Ambio*, **42**, 541–548.
- van Kleunen, M., Dawson, W. & Dostal, P. (2011) Research on invasive-plant traits tells us a lot. *Trends in Ecology and Evolution*, **26**, 317.
- Kueffer, C. & Hirsch Hadorn, G. (2008) How to achieve effectiveness in problem-oriented landscape research: The example of research on biotic invasions. *Living Reviews in Landscape Research*, **2**. <http://www.livingreviews.org/lrlr-2008-2>
- Lambertini, M., Leape, J., Marton-Lefevre, J., Mittermeier, R.A., Rose, M., Robinson, J.G., Stuart, S.N., Waldman, B. & Genovesi, P. (2011) Invasives: a major conservation threat. *Science*, **333**, 404–405.
- Leung, B., Roura-Pascual, N., Bacher, S., Heikkilä, J., Brotons, L., Burgman, M.A., Dehnen-Schmutz, K., Essl, F., Hulme, P.E., Richardson, D.M., Sol, D. & Vilà, M. (2012) TEASing apart alien-species risk assessments: a framework for best practices. *Ecology Letters*, **15**, 1475–1493.
- Light, T. & Marchetti, M.P. (2007) Distinguishing between invasions and habitat changes as drivers of diversity loss among California’s freshwater fishes. *Conservation Biology*, **21**, 434–446.
- Meyerson, L.A. & Reaser, J.K. (2003) Bioinvasions, bioterrorism, and biosecurity. *Frontiers in Ecology and the Environment*, **1**, 307–314.
- Paolucci, E., MacIsaac, H.J. & Ricciardi, A. (2013) Origin matters: alien consumers inflict greater damage on prey populations than do native consumers. *Diversity and Distributions*, **19**, 988–995.
- Pejchar, L. & Mooney, H.A. (2009) Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution*, **24**, 497–504.
- Penman, D.R. (1998) *Managing a leaky border. Towards a bio-security research strategy*. Report 81. Ministry of Research, Science and Technology, Wellington, New Zealand.
- Pyšek, P. & Richardson, D.M. (2010) Invasive species, environmental change and management, and ecosystem health. *Annual Review of Environment and Resources*, **35**, 25–55.
- Rhymer, J.M. & Simberloff, D. (1996) Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, **27**, 83–109.
- Ricciardi, A. (2004) Assessing species invasions as a cause of extinction. *Trends in Ecology and Evolution*, **19**, 619.
- Ricciardi, A. (2007) Are modern biological invasions an unprecedented form of global change? *Conservation Biology*, **21**, 329–336.
- Ricciardi, A. & Atkinson, S.K. (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters*, **7**, 781–784.
- Ricciardi, A. & Simberloff, D. (2009) Assisted colonization is not a viable conservation strategy. *Trends in Ecology & Evolution*, **24**, 248–253.
- Ricciardi, A., Palmer, M.E. & Yan, N.D. (2011) Should biological invasions be managed as natural disasters? *BioScience*, **61**, 312–317.

- Ricciardi, A., Hoopes, M.F., Marchetti, M.P. & Lockwood, J.L. (2013) Progress toward understanding the ecological impacts of non-native species. *Ecological Monographs*, **83**, 263–282.
- Richardson, D.M. (2009) Invasion biology deconstructed. *Trends in Ecology & Evolution*, **24**, 258–259.
- Richardson, D.M. (2011) Invasion science: the roads travelled and the roads ahead. *Fifty years of invasion ecology. The legacy of Charles Elton* (ed. by D.M. Richardson), pp. 397–407. Wiley-Blackwell, Oxford.
- Richardson, D.M. & Gaertner, M. (2013) Plant invasions as builders and shapers of novel ecosystems. *Novel ecosystems: intervening in the new ecological world order* (ed. by R.J. Hobbs, E.C. Higgs and C.M. Hall), pp. 102–114. Wiley-Blackwell, Oxford.
- Richardson, D.M. & Pyšek, P. (2008) Fifty years of invasion ecology – the legacy of Charles Elton. *Diversity and Distributions*, **14**, 161–168.
- Richardson, D.M., Pyšek, P., Simberloff, D., Rejmánek, M. & Mader, A.D. (2008) Biological invasions – the widening debate: a response to Charles Warren. *Progress in Human Geography*, **32**, 295–298.
- Richardson, D.M., Pyšek, P. & Carlton, J.T. (2011) A compendium of essential concepts and terminology in invasion ecology. *Fifty years of invasion ecology. The legacy of Charles Elton* (ed. by D.M. Richardson), pp. 409–420. Wiley-Blackwell, Oxford.
- Rosenzweig, M.L. (2001) The four questions: what does the introduction of exotic species do to diversity. *Evolutionary Ecology Research*, **3**, 361–367.
- Rothlisberger, J.D., Finnoff, D.C., Cooke, R.M. & Lodge, D.M. (2012) Ship-borne nonindigenous species diminish Great Lakes ecosystem services. *Ecosystems*, **15**, 462–476.
- Roy, H.E., Adriaens, T., Isaac, N.J.B., Kenis, M., Onkelinx, T., Martin, G.S., Brown, P.M.J., Hautier, L., Poland, R., Roy, D.B., Comont, R., Eschen, R., Frost, R., Zindel, R., Van Vlaenderen, J., Nedvěd, O., Ravn, H.P., Grégoire, J.-C., de Biseau, J.-C. & Maes, D. (2012) Invasive alien predator causes rapid declines of native European ladybirds. *Diversity and Distributions*, **18**, 717–725.
- Sagoff, M. (2005) Do non-native species threaten the natural environment? *Journal of Agricultural and Environmental Ethics*, **18**, 215–236.
- Salo, P., Korpimaki, E., Banks, P.B., Nordstrom, M. & Dickman, C.R. (2007) Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B*, **274**, 1237–1243.
- Schlaepfer, M.A., Pascal, M. & Davis, M.A. (2011a) How might science misdirect policy? Insights into the threats and consequences of invasive species. *Journal of Consumer Protection and Food Safety*, **6**(Suppl. 1), S27–S31.
- Schlaepfer, M.A., Sax, D.F. & Olden, J.D. (2011b) The potential conservation value of non-native species. *Conservation Biology*, **25**, 428–437.
- Schweiger, O., Biesmeijer, J.C., Bommarco, R. et al. (2010) Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biological Reviews*, **85**, 777–795.
- Sekericioglu, C.H. (2011) Functional extinctions of bird pollinators cause plant declines. *Science*, **331**, 1019–1020.
- Short, J., Kinnear, J.E. & Robley, A. (2002) Surplus killing by introduced predators in Australia – evidence for ineffective anti-predator adaptations in native prey species? *Biological Conservation*, **103**, 283–301.
- Simberloff, D. (2003) Confronting introduced species: a form of xenophobia? *Biological Invasions*, **5**, 179–192.
- Simberloff, D. (2004) A rising tide of species and literature: a review of some recent books on biological invasions. *BioScience*, **54**, 247–254.
- Simberloff, D. (2005) Non-native species do threaten the natural environment! *Journal of Agricultural and Environmental Ethics*, **18**, 596–607.
- Simberloff, D. (2006) Hybridization between native and introduced wildlife species: importance for conservation. *Wildlife Biology*, **2**, 143–150.
- Simberloff, D. (2011) How common are invasion-induced ecosystem impacts? *Biological Invasions*, **13**, 1255–1268.
- Simberloff, D., Alexander, J., Allendorf, F. et al. (2011) Non-natives: 141 scientists object. *Nature*, **475**, 36.
- Simberloff, D., Souza, L., Nuñez, M.A., Barrios-Garcia, M.N. & Bunn, W. (2012) The natives are restless, but not often and mostly when disturbed. *Ecology*, **93**, 598–607.
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E. & Vilà, M. (2013) Impacts of biological invasions – what's what and the way forward. *Trends in Ecology and Evolution*, **28**, 58–66.
- Stinson, K.A., Campbell, S.A., Powell, J.R., Wolfe, B.E., Callaway, R.M., Theen, G.C., Hallett, S.G., Prati, D. & Klironomos, J.N. (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biology*, **4**, e140. 727–731.
- Strauss, S.Y., Webb, C.O. & Salamin, N. (2006) Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences USA*, **103**, 5841–5845.
- Thomas, C.D. (2013) The Anthropocene could raise biological diversity. *Nature*, **502**, 7.
- Thompson, K. & Davis, M.A. (2011) Why research on traits of invasive plants tells us very little. *Trends in Ecology and Evolution*, **26**, 155–156.
- Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology and Evolution*, **21**, 208–216.
- Valéry, L., Fritz, H. & Lefevre, J.-C. (2013) Another call for the end of invasion biology. *Oikos*, **122**, 1143–1146.
- Vermeij, G.J. (2005) Invasion as expectation. *Species invasions: insights into ecology, evolution, and biogeography* (ed. by D.F. Sax, J.J. Stachowicz and S.D. Gaines), pp. 315–339. Sinauer Associates, Sunderland, Massachusetts.
- van der Wal, R., Truscott, A.-M., Pearce, I.S.K., Cole, L., Harris, M.P. & Wanless, S. (2008) Multiple anthropogenic

- changes cause biodiversity loss through plant invasion. *Global Change Biology*, **14**, 1428–1436.
- Warren, C.R. (2007) Perspectives on the ‘alien’ versus ‘native’ species debate: a critique of concepts, language and practice. *Progress in Human Geography*, **31**, 427–446.
- Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J. & Richardson, D.M. (2009a) Biogeographic concepts define invasion biology. *Trends in Ecology and Evolution*, **24**, 586.
- Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J. & Richardson, D.M. (2009b) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology & Evolution*, **24**, 136–144.
- Wyatt, K.B., Campos, P.F., Gilbert, M.T.P., Kolokotronis, S.-O., Hynes, W.H., DeSalle, R., Daszak, P., MacPhee, R.D.E. & Greenwood, A.D. (2008) Historical mammal extinction on Christmas Island (Indian Ocean) correlates with introduced infectious disease. *PLoS ONE*, **3**, e3602.