

Short Note

Concerning invasive species: Reply to Brown and Sax

PHILLIP CASSEY,^{1*} TIM M. BLACKBURN,¹ RICHARD P. DUNCAN² AND STEVEN L. CHOWN³

¹*School of Biosciences, Birmingham University, Edgbaston B15 2TT, UK (Email: p.cassey@bham.ac.uk)*, ²*Ecology and Entomology Group, Lincoln University, Canterbury, New Zealand* and ³*Centre for Invasion Biology, Stellenbosch University, Matieland, South Africa*

Abstract Biological invasions have commonly occurred, and to a lesser degree continue to do so, without human assistance. It is, however, a combination of the rate and magnitude, as well as the distances and agency involved, that separates human-driven invasion processes from self-perpetuated colonization events. Exotic species are a pervasive and major component of human-induced global change. Decisions to manage invasive species will require judgements to be communicated from scientists to policy makers, because scientists may often be the only ones in the position to make them.

Key words: biological invasion, ecosystem functioning, exotic species, mass extinction event, scientific role.

INTRODUCTION

In a recent essay, Brown and Sax (2004) addressed a variety of topics concerning invasive species. At the heart of their discussion was their concern regarding the ‘visceral emotional response’ that invasive species tend to elicit among people. They compared this response to an attitude of xenophobia supposedly common among humans in which we ‘treat foreigners . . . with distrust, dislike, even loathing’. While the authors did not advocate the continuing introduction of non-native species, they did argue for what they regard as greater ‘scientific objectivity and less emotional xenophobia’ in the study of invasive species. They pointed out that invasion is a natural process, just as is extinction, and that in these regards ‘the earth has previously experienced changes of a magnitude equal to or exceeding those caused by recent human activities’. Invasive species may provide valuable insights into a range of biological questions. Brown and Sax concluded that scientific questions about the causes and consequences of biological invasions should be separated from moral and social questions about the desirability of such invasions, and that it is ‘up to humankind as a whole to decide whether it [biological invasion] is good or bad, and hence what actions should be taken’.

We find much to agree with in Brown and Sax (2004). However, we think that several of their arguments require further consideration, which has

prompted this response. Here, we address three issues. First, we consider comparisons between invasions (and related extinctions) as natural *versus* anthropogenic events. Second, we consider the implications of current events for biodiversity. Third, we discuss the role of scientists in studying the processes that have resulted from the transportation and establishment of non-native species.

NATURAL *VERSUS* ANTHROPOGENIC EVENTS

Brown and Sax observe that ‘biological invasions are nothing new’, and that ‘the earth has experienced many invasions, sometimes in waves of many species, and often in independent single-species colonization events’. They note that the same is true for extinctions, that many prehuman extinctions can be attributed to prehuman invasions, and that many prehuman extinction and invasion events were of at least comparable magnitude to the current one. We think that this view misrepresents the uniqueness of the current events, at least for invasions, in several ways.

First, the current mass invasion event (we use this terminology for parity with the current mass extinction event) is vastly greater in geographical extent than any single event that we know about (or can infer) from the geological past. Our best guess is that there is not a single landmass that is unaffected, from the most biodiverse continent to the most isolated oceanic island. For example, although Antarctica and its surrounding islands are amongst the most isolated places

*Corresponding author.

Accepted for publication December 2004.

on earth, they now play host to a wide variety of human-introduced species, including marine, freshwater and terrestrial microorganisms, plants, invertebrates and vertebrates, which in several cases are causing widespread changes to these systems (reviewed in Frenot *et al.* 2005). Across the sub-Antarctic islands, which are distributed widely over the Southern Ocean, and differ substantially in the communities they host, many of these colonizers are the same Palaearctic weedy species (Greve *et al.* 2005). This sets the current invasion event apart from events like the Great American Interchange, which only concerned a pair of continents (and a few offshore islands), or recolonization after glaciation, which mainly concerned only the far north (and, we would note, was only a replacement of the little that the glaciers left behind). If all the examples of prehuman invasion that Brown and Sax quoted had occurred simultaneously we would be getting closer in extent to the current event.

Second, the current mass invasion event is unusual in the distance over which invasions have occurred (and indeed are occurring). Natural long-distance dispersal events are not uncommon. For example, vagrant North American birds arrive annually on European shores (and vice versa) after crossing the Atlantic. However, while that exchange must have been occurring for centuries, it has not obviously resulted in colonization. Yet, in the last 150 years 12 species of British passerine bird have established viable populations in New Zealand, antipodal to Britain and well beyond the natural colonization abilities of all but the most exceptional vertebrate species. New Zealand also houses 25 non-volant terrestrial mammal species (excluding humans), established in the last 800 years on islands that no non-volant terrestrial mammal had naturally colonized in 80 million years.

The one natural long-distance colonization event cited by Brown and Sax (2004) concerned the cattle egret, which arguably is an event that has only occurred because of the facilitating effects of humans (e.g. introducing large grazing mammals, and destroying habitat and introducing plant species to accommodate them). The one example of non-anthropogenic global colonization that we can think of concerns the tendency for unicellular organisms to be global in their distribution (Fenchel & Finlay 2004). However, this is also contentious (Franzmann 1996; Lachance 2004; and references therein).

Third, the current mass invasion event is unusual in the timescale over which invasions have occurred. Brown and Sax cite the example of rapid tree recolonization following the retreat of the glaciers: 'within a few thousand years, tree species had spread hundreds of kilometres from glacial refugia to occupy their current ranges'. Those rapid events seem positively pedestrian in comparison to events such as the rapid

colonization of the Black Sea by the American comb jelly, *Mnemiopsis leidyi* (Carlton 2000), the virtually global spread of the isopod *Porcellio scaber* over a few hundred years (Wang & Schreiber 1999; Slabber & Chown 2002) and the invasion by pines of the southern hemisphere over the past 50 years (Richardson & Higgins 1998). Brown and Sax do cite an example of faster colonization, but since this refers to spread of bird species into agricultural habitat it is hardly a convincing historical precedent.

The relative rates of natural and anthropogenic colonization have been quantified for the pterygote insect fauna of Gough Island by Gaston *et al.* (2003). They found that 71 of the 99 species recorded from Gough were established introductions, even though Gough has only been landed on approximately 233 times in the 325 years since its discovery by humans. This suggests a successful establishment rate of 218 exotic species per thousand years. Gough island is estimated to be 2–3 million years old, and 21 colonization events could account for the indigenous fauna (Gaston *et al.* 2003). Assuming uniform colonization rates over the past two million years, this amounts to one colonization every 95 000 years, but if it is assumed that 95% of indigenous species have gone extinct over the period, the rate increases to one successful colonization per millennium. Thus, rates of anthropogenic introduction are still two to three orders of magnitude greater than background levels of net colonization for the island.

Fourth, the current mass invasion event is unusual in the agency of dispersal. Natural colonization events rely on the dispersal powers of the organisms themselves, which for many taxa are limited. Moreover, arriving at a new site is just the first hurdle that needs to be overcome: individuals of sexual species then need to find mates. Although there are examples of natural colonization events resulting from the arrival of large propagules (e.g. Clegg *et al.* 2002), most natural propagule sizes are likely to be small (one or two individuals) and (as we noted above) infrequent. These founders then have to survive the perils that bedevil small populations, such as demographic stochasticity, environmental stochasticity and inbreeding. In contrast, human-mediated dispersal events frequently concern large numbers of individuals, or repeated releases that are often directly introduced to suitable habitat. Exotic pasture weeds that are dispersed as pasture seed contaminants, for example, end up being sown in their ideal pasture habitat. This much higher propagule pressure and habitat matching means that the problems of small populations are greatly reduced (Williamson 1996), as larger releases ameliorate demographic stochasticity and inbreeding (but see Briskie & Mackintosh 2004) while repeated releases ameliorate environmental stochasticity (Lockwood *et al.* 2005). While difficult to test (but see Gaston

et al. 2003), it seems likely that the probability of successful establishment is greatly enhanced as a result.

Brown and Sax are not the first to note that extinction and invasion are natural processes. The literature frequently compares exotic establishment to natural colonization and it is therefore simply a combination of the rate and magnitude, as well as the distances and agency involved, that separates human-driven invasion processes from self-perpetuated colonization events. The earth's present biodiversity took hundreds of millions of years to evolve, with each land mass as home to different biotas. Now, every major zoo in the world can have an elephant (the largest terrestrial mammal) thanks to the ease with which species, of all shapes and sizes, are transported. The extent of this human-induced biotic exchange would be limitless if it wasn't for the fact that, despite our efforts, not all species transported and released have successfully established.

We do concede that the current mass extinction event pales into insignificance compared to mass events in the geological past. However, we do not find it particularly reassuring that our role in driving extinctions globally does not yet approach that of an asteroid impact. As Brown and Sax point out, in some places it virtually does.

CONSEQUENCES OF ANTHROPOGENIC INVASIONS

If current human-driven invasions are not simply the modern expression of a natural process, it follows that the consequences of those invasions should also differ from those of natural colonization events. One expression of this is in the decrease in the distinctiveness of biotas in different biogeographical regions.

Species recently lost to extinction tend to be range-restricted local endemics, and so unique to local areas (e.g. single islands) (Lawton & May 1995). For example, there is a positive relationship between taxonomic level of endemism and probability of extinction for bird species inhabiting New Zealand at the time of first human colonization (McDowall 1969; Duncan & Blackburn 2005). By contrast, successful invaders tend to be more widely distributed than species that fail to establish exotic populations (e.g. Blackburn & Duncan 2001a), while some species have repeatedly invaded a range of exotic locations (e.g. Long 1981, 2003). These patterns are resulting in biotic homogenization (Elton 1958; Lockwood & McKinney 2001). Thus, 800 years ago Britain and New Zealand shared no breeding bird species in common. Now they share 37 (Blackburn & Duncan 2001b). In that same period New Zealand lost 62 breeding bird species, or almost half of its avifauna, mainly driven extinct by exotic mammalian predators (Blackburn & Gaston 2005; Duncan & Blackburn 2005). A unique fauna shaped

by evolution over 80 million years has now been transformed such that, over much of New Zealand, most of the birds that a visitor from the UK encounters are the same as back home. The same is true for floras and faunas around the world. It is the biological equivalent of flying from Seattle to Paris and going to Starbucks for your coffee.

When discussing the loss and gain of species among regions we frequently refer to the term 'biodiversity'. In its simplest definition, biodiversity refers to the number of species per unit area. However, it is obvious that this definition does not satisfactorily account for the diversity of life (Purvis & Hector 2000), or for the processes of ecological interaction and evolution that maintain existing species and are critical for generating new life (Bøhn & Amundsen 2004). Homogenization may not result in biodiversity loss in terms of simple numbers, but may do so significantly in terms of identities (see also Vane-Wright *et al.* 1991) and ecosystem processes (Loreau *et al.* 2001; Kinzig *et al.* 2002). For example, it has been suggested that different species perform the same functional role in ecosystems such that changes in species diversity should not necessarily affect ecosystem functioning ('functional redundancy': Lawton & Brown 1993). However, several controlled experiments have instead found evidence of functional complementarity, resulting from processes such as resource partitioning and facilitation, among at least some of the species involved (e.g. Hector *et al.* 1999; Cardinale *et al.* 2002). Thus, species turnover through homogenization may be far from positive in terms of altering the functional ability of ecosystems in ways that remain exceedingly difficult to predict.

Brown and Sax correctly point out that many of the ecosystems that are currently being impacted by humans have already been greatly modified by human intervention in the past. Thus, the notion of 'pristine' ecosystems should largely be discarded (Gaston & Blackburn 2003). Yet, that is not to equate past and current human influences. Aboriginal cultures were certainly responsible for many extinctions (e.g. Milberg & Tyrberg 1993), but for exotic introductions the rates of transport, distances traversed and numbers of species involved have all increased dramatically since the initial period of European exploration (e.g. Pimm *et al.* 1995).

Thus, we think it a questionable choice of language when Brown and Sax describe losses to extinction as being 'more than offset' by the gains from invasion. It is not clear to us that they are, in any sense except in terms of pure local species numbers. Yet, in the accountancy of global change, simply totting up the net change in species numbers is probably the least useful way of assessing profit and loss. Moreover, we would note that choice of the term 'more than offset' is no less value-laden than the emotive language that Brown and Sax argue against. It implies to us a posi-

tive benefit of biotic homogenization with which we think few scientists would agree. This brings us to our final set of points.

THE ROLE OF SCIENTISTS

Brown and Sax state that the aim of their essay 'is not to suggest that modern humans should let nature take its course and elect not to intervene in the dynamics of dispersal and extinction, and the resulting impacts on biodiversity, ecosystem function and the economy'. However, that statement raises a number of important questions, perhaps most notably why should humans intervene, when and how? We believe that these are rightly questions for scientists. Only with the benefit of the knowledge provided by rigorous, impartial and objective science can society (or its elected representatives) take informed decisions over what action to take best to manage the environment for biodiversity, ecosystem function and the economy (with their concomitant effects of 'quality of life').

Moreover, while Brown and Sax argue that 'deciding what is good or bad is a moral and social issue', we see questions of 'good' and 'bad' as equally valid in a scientific context. For example, if the question is 'what is the impact of invasive species on the ability of a plant community to recover after drought?' or 'what is the impact of invasive species on the health of the human population of a country?', there are clear grounds for equating answers in the negative as 'bad'. Certainly, management decisions based on the answers to such questions will require value judgements to be communicated from scientists to policy makers, because scientists may often be the only ones in the position to make them. Thus, it would seem to us to be the responsibility of science to inform society. (Indeed, it has often been argued that the exasperation voiced by scientists over the poor level of scientific literacy in the general public, and the poor level of scientific debate in the media, is precisely because that communication is currently inadequate.) And given that policy makers are quite willing to ignore those scientific value judgements even when they are clearly communicated (e.g. in failing to ratify the Kyoto Protocol, or denying a connection between HIV and AIDS), the idea that such decisions will be taken on the basis of the raw facts is naïve at best.

As scientists, however, we also recognize that the processes which form and structure ecological assemblages are incompletely understood and remain controversial (e.g. Lawton 1999; Chave 2004; Simberloff 2004a; Gaston & Chown 2005). Exotic species are pervasive, and studying their evolutionary ecology and the consequences of their successful establishment is one way in which an understanding of these processes may be advanced: indeed, the explosion of interest in

the study of invasive species has itself been compared to an 'invasion' of the scientific literature (Simberloff 2004b). We agree with Brown and Sax that invasive species are an opportunity to be exploited, albeit an opportunity that we do not think will be impaired by a growing environmental awareness to 'stem the tide' of invading exotic species. It is encouraging at this point in history to believe that invasions really could be a force for good. Nevertheless, regardless of whether we consider invasions (and extinctions) 'good' or 'bad', we study them, and are funded to do so in part (and we believe for good reason) because it is widely concluded that they are undesirable for maintaining the function of natural ecological and evolutionary patterns and processes. How many funding applications propose studying invasive species for their intrinsic interest alone?

When people treat foreigners 'with distrust, dislike, even loathing', it is because they believe that those foreigners are a threat, be that to their possessions, livelihoods, quality or way of life, or perhaps even to their life itself. With notable exceptions – invading armies, for instance – those threats are more imagined than real. That is not the case for biological invasions, which have been (and continue to be) a genuine threat to the livelihoods, way of life and life itself, of populations and species on every landmass on earth (see also Simberloff 2003). It is possible for scientists to study these processes with objectivity, but we should not confuse scientific objectivity with moral neutrality. After all, Albert Einstein laid the foundation for the development of nuclear weapons, yet argued for nuclear disarmament. His standing is not diminished as a result. Consequently, we congratulate any individual who, like Marilyn Fox (Brown & Sax 2004), against the flood (an unabashedly emotive term for a large order or magnitude of particles) of non-native species, still has the strength to believe it is worthwhile to stop the car and pull out exotic plant pest species in a region specifically preserved for natural heritage.

In conclusion, species have gone and are going extinct (Lawton & May 1995). Most recent extinctions can be attributed to drivers of human-induced global change (Avisé 2003). One of these drivers, which is leading to local and global extinction, is the transportation and establishment of exotic species (Vitousek *et al.* 1997). In addition, when the dual processes of extinction and invasion overlap in a common region they can lead to increased biological homogenization where species similarity increases (and species distinctiveness decreases) among a set of communities through time (McKinney & Lockwood 1999; Olden & Poff 2003). Scientists have not yet provided any compelling evidence that either of these processes is slowing down, although the rates and magnitudes are indeed changing among some taxa. The fact that we can look forward to ecological systems recovering from

these assaults in the next 10 million years or so is not one that we consider a great consolation.

ACKNOWLEDGEMENTS

P.C. is supported by the Leverhulme Trust (Grant F/00094/AA). S.L.C. is supported by the DST Centre of Excellence for Invasion Biology. We are grateful to Doug Armstrong, Julie Lockwood, Kevin Parker, Dan Simberloff and Yvan Richard for comments on the final manuscript.

Finally, we would like to thank Jim Brown and Dov Sax for stimulating this manuscript and our ongoing discussions regarding the nature and processes of biological invasions.

REFERENCES

- Awise J. C. (2003) The best and the worst of times for evolutionary biology. *Bioscience* **53**, 247–55.
- Blackburn T. M. & Duncan R. P. (2001a) Determinants of establishment success in introduced birds. *Nature* **414**, 195–7.
- Blackburn T. M. & Duncan R. P. (2001b) Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *J. Biogeogr.* **28**, 927–39.
- Blackburn T. M. & Gaston K. J. (2005) Biological invasions and the loss of birds on islands: insights into the idiosyncrasies of extinction. In: *Exotic Species: A Source of Insight into Ecology, Evolution, and Biogeography* (eds D. F. Sax, S. D. Gaines & J. J. Stachowicz). Sinauer, Sunderland, MA.
- Böhn T. & Amundsen P.-A. (2004) Ecological interactions and evolution: forgotten parts of biodiversity? *Bioscience* **54**, 804–5.
- Briskie J. V. & Mackintosh M. (2004) Hatching failure increases with severity of population bottlenecks in birds. *Proc. Natl. Acad. Sci. USA* **101**, 558–61.
- Brown J. H. & Sax D. F. (2004) An essay on some topics concerning invasive species. *Austral Ecol.* **29**, 530–6.
- Cardinale B. J., Palmer M. A. & Collins S. C. (2002) Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**, 426–9.
- Carlton J. T. (2000) Global change and biological invasions in the oceans. In: *Invasive Species in a Changing World* (eds H. A. Mooney & R. J. Hobbs) pp. 31–53. Island Press, Washington DC.
- Chave J. (2004) Neutral theory and community ecology. *Ecol. Lett.* **7**, 241–53.
- Clegg S. M., Degnan S. M., Kikkawa J., Moritz C., Estoup A. & Owens I. P. F. (2002) Genetic consequences of sequential founder events by an island-colonizing bird. *PNAS* **99**, 8127–32.
- Duncan R. P. & Blackburn T. M. (2004) Extinction and endemism in the New Zealand avifauna. *Global Ecol. Biogeogr.* **13**, 509–17.
- Elton C. S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- Fenchel T. & Finlay B. J. (2004) The uniqueness of small species: patterns of local and global diversity. *Bioscience* **54**, 777–84.
- Franzmann P. D. (1996) Examination of Antarctic prokaryotic diversity through molecular comparisons. *Biodivers. Conserv.* **5**, 1295–305.
- Frenot Y., Chown S. L., Whinam J., Selkirk P. M., Convey P., Skotnici M. & Bergstrom D. M. (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biol. Rev.* **80**, 45–72.
- Gaston K. J. & Blackburn T. M. (2003) Macroecology and conservation biology. In: *Macroecology: Concepts and Consequences* (eds T. M. Blackburn & K. J. Gaston) pp. 345–67. Blackwell Science, Oxford.
- Gaston K. J. & Chown S. L. (2005) Neutrality and the niche. *Funct. Ecol.* **19**, 1–6.
- Gaston K. J., Jones A. G., Hänel C. & Chown S. L. (2003) Rates of species introduction to a remote oceanic island. *Proc. R. Soc. Lond. B* **270**, 1091–8.
- Greve M., Gremmen N. J. M., Gaston K. J. & Chown S. L. (2005) Nestedness of Southern Ocean island biotas: ecological perspectives on a biogeographic conundrum. *J. Biogeogr.* **32**, 155–68.
- Hector A., Schmid B., Beierkuhnlein C. *et al.* (1999) Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123–7.
- Kinzig A. P., Pacala S. W. & Tilman D., eds. (2002) *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. Princeton University Press, Princeton.
- Lachance M.-A. (2004) Here and there or everywhere? *Bioscience* **54**, 884.
- Lawton J. H. (1999) Are there general laws in ecology? *Oikos* **84**, 177–92.
- Lawton J. H. & Brown V. K. (1993) Redundancy in ecosystems. In: *Biodiversity and Ecosystem Function* (eds E. D. Schulze & H. A. Mooney) pp. 255–70. Springer, New York.
- Lawton J. H. & May R. M., eds. (1995) *Extinction Rates*. Oxford University Press, Oxford.
- Lockwood J. L. & Mckinney M. L., eds. (2001) *Biotic Homogenization*. Kluwer Academic, New York.
- Lockwood J. L., Cassey P. & Blackburn T. M. (2005) The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* **20**, 223–8.
- Long J. L. (1981) *Introduced Birds of the World*. David and Charles, London.
- Long J. L. (2003) *Introduced Mammals of the World*. CSIRO Publishing, Melbourne.
- Loreau M., Naeem S., Inchausti P. *et al.* (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–8.
- McDowall R. M. (1969) Extinction and endemism in New Zealand land birds. *Tuatara* **17**, 1–12.
- McKinney M. L. & Lockwood J. L. (1999) Biotic homogenization: a few winners replacing may losers in the next mass extinction. *Trends Ecol. Evol.* **14**, 450–3.
- Milberg P. & Tyrberg T. (1993) Naïve birds and noble savages – a review of man-caused prehistoric extinctions of island birds. *Ecography* **16**, 229–50.
- Olden J. D. & Poff N. L. (2003) Toward a mechanistic understanding and prediction of biotic homogenization. *Am. Nat.* **162**, 442–60.
- Pimm S. L., Moulton M. P. & Justice L. J. (1995) Bird extinctions in the central Pacific. In: *Extinction Rates* (eds J. H. Lawton & R. M. May) pp. 75–87. Oxford University Press, Oxford.
- Purvis A. & Hector A. (2000) Getting the measures of biodiversity. *Nature* **405**, 212–19.
- Richardson D. M. R. & Higgins S. I. (1998) Pines as invaders in the southern hemisphere. In: *Ecology and Biogeography of*

- Pinus* (ed. D. M. Richardson) pp. 450–73. Cambridge University Press, Cambridge.
- Simberloff D. (2003) Confronting introduced species: a form of xenophobia? *Biol. Invas.* **5**, 179–92.
- Simberloff D. (2004a) Community ecology: is it time to move on? *Am. Nat.* **163**, E1–E13.
- Simberloff D. (2004b) A rising tide of species and literature: a review of some recent books on biological invasions. *Bio-science* **54**, 247–54.
- Slabber S. & Chown S. L. (2002) The first record of a terrestrial crustacean, *Porcellio scaber* (Isopoda, Porcellionidae), from sub-Antarctic Marion Island. *Polar Biol.* **25**, 855–8.
- Vane-Wright R. I., Humphries C. J. & Williams P. H. (1991) What to protect? – Systematics and the agony of choice. *Biol. Conserv.* **55**, 235–54.
- Vitousek P. M., D'Antonio C. M., Loope L. L., Rejmanek M. & Westbrooks R. (1997) Introduced species: a significant component of human-caused global change. *NZ J. Ecol.* **21**, 1–16.
- Wang M. & Schreiber A. (1999) Population genetics of the woodlouse *Porcellio scaber* Latr. (Isopoda: Oniscoidea) in central Europe: passive dispersal and postglacial range expansion. *Can. J. Zool.* **77**, 1337–47.
- Williamson M. (1996) *Biological Invasions*. Chapman & Hall, London.