## ECOLOGICAL SOUNDING

# The paradox of invasion

DOV F. SAX and JAMES H. BROWN   *Department of Biology, University of New Mexico, Albuquerque, NM 87131, U.S.A. E-mail: jhbrown@unm.edu*

**ABSTRACT**

It is paradoxical that exotic species invade and displace native species that are well adapted to local environments. Yet, even those exotics that eventually become abundant and widespread, often do so only after having failed to establish following multiple earlier introductions. The first pattern, while not generally discussed in this context, is usually explained by exotic species pre-adaptations for human-altered environments and by a release from enemies. It can be understood further by examining the superior quality of colonists from large species-rich regions and the historical contingency of evolution. The second pattern is generally explained by invoking demographic and environmental stochasticity; however, it can be understood further by examining the role of environmental variation over space and by metapopulation dynamics. These processes provide a context in which these patterns of invasion are not paradoxical, but instead, expected.

**Key words** Demographic stochasticity, environmental stochasticity, exotic species, insular taxon cycles, introduced species, susceptibility to invasion.

## INTRODUCTION

Invasions of alien species present ecologists and evolutionary biologists with an interesting paradox: why are exotic organisms, which come from distant locations and have had no opportunity to adapt to the local environment, able to become established and sometimes to displace native species, which have had a long period of history in which to adapt to local conditions? Another version of this paradox is the insular taxon cycle, in which successive waves of newly colonizing species from distant origins are postulated ultimately to replace previous inhabitants (Wilson, 1961; Ricklefs & Cox, 1972, 1978).

There is an extensive literature on both exotic species and island biology (exotics: e.g. Elton, 1958; Baker, 1965; Carlton, 1979; Ebenhard, 1988; Drake *et al.*, 1989; Hengeveld, 1989; Williamson, 1996; islands: e.g. Wallace, 1880; Carlquist, 1965, 1974; Williamson, 1981; Brown & Lomolino, 1998). Much of this literature implicitly addresses the above paradox, most notably by considering the characteristics of invading species that make them good colonists, and the characteristics of invaded environments that make them susceptible to establishment by aliens. Characteristics of successful invaders often include: broad ecological requirements and tolerances, sometimes reflected in large geographical ranges (e.g. Baker, 1965; Forcella & Wood, 1984; Moulton & Pimm, 1986; Crawley, 1987; Rejmánek, 1996); *r*-selected life histories (e.g. Baker, 1965); associations with disturbed or anthropogenic habitats (e.g. Baker, 1965; Stebbins, 1965); and origins from large continents with diverse biotas (e.g. Darwin, 1859; Elton, 1958). Characteristics of invaded environments often include: geographical and historical isolation (e.g. Elton, 1958; Brown, 1989); low diversity of native species (e.g. Elton, 1958; Fox & Fox, 1986; Case, 1990); high levels of natural disturbance or human activities (e.g. Elton, 1958; Frankel, 1977; Fox & Fox, 1986; Burke & Grime, 1996; Case, 1996; Suarez *et al.*, 1998);

*Correspondence: Dov F. Sax, Department of Ecology, Evolution & Marine Biology, University of California, Santa Barbara, CA 93106, U.S.A. E-mail: sax@lifesci.ucsb.edu*

and absence of co-adapted enemies, including competitors, predators, herbivores, parasites and diseases (e.g. Elton, 1958; Ricklefs & Cox, 1972, 1978; Newsome & Noble, 1986). Except for the insular taxon cycle, however, these characteristics are usually not discussed in the context of invasion being paradoxical.

It is not our purpose here to review the extensive literature on invasive species and invaded environments. Instead, this commentary focuses on the paradox. Many of the above characteristics can be reinterpreted in terms of resolving the paradox. We emphasize two phenomena that appear to offer insights. One is the fact that species that eventually become abundant and widespread, often do so only after having failed to establish following multiple earlier introductions. The other is the fact that alien species, with no evolutionary history in the local environment, are able not only to become established, but often to become dominant and to displace native species.

## SUCCESSFUL ESTABLISHMENT FOLLOWING MULTIPLE FAILURES

A common phenomenon frequently noted in the literature on exotic species is that most introductions fail (e.g. Veltman *et al.*, 1996). This is true even for species that eventually become established and highly successful in an invaded region. For example, the European red deer, *Cervus elaphus* L., was introduced to New Zealand and spread over the entire South Island, becoming a serious economic problem, but only after 31 previous introductions had failed (Clarke, 1971). Similarly, the European Starling, *Sturnus vulgaris* L., has become one of the most abundant and widespread bird species in North America, but prior to its successful establishment in 1895 at least eight previous introductions had failed (Lever, 1985). Although less well-documented, this same phenomenon is also true of natural colonization. For example, in a paper entitled 'The role of the "accidental"', Joseph Grinnell (1922) called attention to the frequent observations of bird species far from the known limits of their geographical ranges. There are frequent sightings of non-native bird species on islands, even such isolated ones as the Hawaiian and Galapagos Archipelagoes (e.g.

Lack, 1970). So why, regardless of whether such immigrants dispersed under their own power or with human assistance, do the vast majority of them fail to establish?

The answer usually given is some combination of demographic and environmental stochasticity. Demographic stochasticity involves the random changes in birth and death rates and the resulting fluctuations in populations due to intrinsic processes such as variation in age structure and sex ratio (Shaffer, 1981, 1987). Even when environmental conditions are favourable, such that large populations would have positive growth rates, such demographic variation can cause the extinction of small local populations of introduced exotics or natural colonists (e.g. Gilpin & Soulé, 1986; Lande, 1988; Simberloff, 1988; Mack, 1995). This can be exacerbated by an Allee effect, the negative effect of population size on population growth when the number of individuals is small. Additionally, environmental stochasticity can cause small colonies to fail. Apparently random temporal fluctuations in the extrinsic environment, including the effects of such things as severe storms, droughts and biotic interactions, can lead to negative growth rates and ultimately to extinctions (e.g. Simberloff, 1988; Lande, 1988; Mack, 1995).

While we recognize the potential roles of demographic and environmental stochasticity, we call attention to two other phenomena that may also account for failed introductions. One is spatial environmental variation. Even species that are abundant and widely distributed are rare or absent at most of the locations within their geographical ranges (Brown *et al.*, 1995; Brown *et al.*, 1996). This implies that many sites are marginal or unsuitable. By marginal we mean that local abiotic and biotic conditions are suboptimal, such that only a small number of individuals can be supported. This also implies that birth rates are low in marginal environments. They may even be lower than death rates, so that the population is a 'sink', supported by continual immigration (Grinnell, 1922; Shmida & Wilson, 1985; Pulliam, 1988). The existence of so many marginal and unsuitable sites within the ranges of even the most widespread and abundant species suggests that most local introductions would fail, because propagules would tend by chance to be introduced into such locations.

Successful establishment is likely to occur only in the relatively unlikely circumstance in which a propagule is introduced to a highly suitable local environment. This can be thought of as the spatial analogue of environmental stochasticity, which traditionally has been concerned only with temporal variation.

The other phenomenon that may account for failed introductions is the dispersal of individuals over space and time. In this category we include effects of metapopulation and source-sink dynamics, but also other processes. Following initial colonization, dispersal away from the site of introduction can reduce population growth, exacerbate Allee effects, and contribute to demographic stochasticity. Evidence for the importance of this process comes from the apparently strong selection for the reduction or loss of dispersal structures in many island plants (e.g. Carlquist, 1965, 1974). On the other hand, once a species has become established in multiple sites, dispersal can play a major role in the persistence of local populations. Then, immigration can 'rescue' populations from extinction due to demographic or environmental stochasticity (Brown & Kodric-Brown, 1977). Established species with a substantial geographical range are sustained in part by the positive feedback effects of dispersal on local population dynamics. Lacking such opportunity for rescue, single, newly established populations are more susceptible to extinction.

## WHY ALIENS DO BETTER THAN NATIVES

A second phenomenon noted in the literature on exotics is that some species not only become established, but also become so abundant and widespread that they dominate certain habitats and sometimes even displace native species. For example, ice-plant, *Mesembryanthemum crystallinum* L., in California and cheat grass, *Bromus tectorum* L., in the western United States have replaced native species and become virtual monocultures in many locations (Vivrette & Muller, 1977; Mack, 1981). In some cases, exotics effectively become 'keystone species', causing reorganization of biotic interactions and changes in ecosystem processes (D'Antonio & Vitousek, 1992). For example, introduction of the brown tree snake, *Boiga irregularis* Cogger, into Guam initiated a cascade of interactions and contributed to the decline or extinction of at least 12 native bird species (Fritts & Rodda, 1998). In Hawaii, the introduction of a nitrogen fixing shrub, *Myrica faya* Ait., enriched soil nutrients on recent lava flows, facilitating the further invasion of additional exotic plant species (Vitousek *et al.*, 1987; Vitousek & Walker, 1989).

Here we consider briefly the two explanations that have traditionally been offered for this phenomenon. Then we add two additional mechanisms that have not been emphasized.

### Novel environments

Many investigators have noted that invading species are particularly successful in disturbed habitats, especially those altered by human activities, i.e. in environments that are novel for native species. Thus, for example, exotic plants in many geographical regions include a large proportion of 'weeds' that occur in agricultural fields, along roadsides, and around settlements (e.g. Elton, 1958; Baker, 1965; Frankell, 1977). Many of the most successful animal invaders are human commensals, such as the house fly, *Musca domestica* L., common cockroach, *Periplaneta americana* L., house sparrow, *Passer domesticus* L., house mouse, *Mus musculus* L. and Norwegian rat, *Rattus norvegicus* Berkenhout; these have become virtually cosmopolitan, following human settlers throughout the world (Elton, 1958; Lever, 1985, 1987). The explanation offered for the success of these species is that they have a long history of association with humans and human-modified ecosystems, and consequently are superior to native species in these environments (e.g. Elton, 1958; Stebbins, 1965). Thus, these exotics have colonized human-altered environments that they are adapted to, but to which native species are not, rather than invading undisturbed habitats and displacing locally adapted native species.

### Release from enemies

The second explanation commonly given is that aliens are released from many biotic interactions. Not only do they typically leave most of their enemies behind when they colonize a distant site, but they also encounter assemblages of

species that have not specialized to interact with them. Furthermore, they have an advantage in competition with native species, whose performance may be reduced by interaction with substantial numbers of co-evolved competitors, predators, parasites and diseases (Ricklefs & Cox, 1972, 1978). Examples of release from biotic interactions are prevalent in the literature. Most of them document the effects of release from specific enemies, often evidenced by increased biological control of the exotic when a co-evolved enemy from its native range is subsequently introduced. Cases include the limiting affects of competitors (e.g. anolis lizards in the Lesser Antilles, Roughgarden, 1983), and predators, herbivores, parasites and diseases (e.g. control of cactus, *Opuntia inermis* (DC.) A. Cunn ex DC. and *O. stricta* (Haw.) Haw., by *Cactoblastis argenteum* in Australia, Dodd, 1959; control of Klamath weed, *Hypericum perforatum* L., by the leaf-eating beetle, *Chrysolina quadrigemina* Suffrian, in western North America, Huffaker & Kennett, 1959; Harris *et al.*, 1969; and control of rabbits by *Myxoma* virus in Australia, Fenner & Ratcliffe, 1965).

There has been less emphasis on the effects of diffuse interactions with multiple species of enemies. Such relationships are more difficult to document, in part because biological control programmes have not generally utilized multiple agents to combat exotics out of concern for unanticipated negative effects on native biota (but see Murdoch *et al.*, 1985). There is, however, indirect evidence for the importance of diffuse interactions. For example, both house sparrows, *P. domesticus*, and starlings, *S. vulgaris*, have fewer parasite species in their exotic range in North America than in their native range in Europe (Hair & Forrester, 1970; Brown & Wilson, 1975). Other probable examples are the successes of closely related species when introduced into another's geographical range (e.g. Schierenbeck *et al.*, 1994). Such differential success is likely due to different combinations of co-evolved enemies, which reduce performance and hence competitive ability within the native range. Diffuse interactions with multiple enemies may also explain why only a small number of species have been able to invade undisturbed environments on continents in the tropics (Rejmánek, 1996). Such low invasibility

may be due to biotic resistance from the diverse native biota. This conjecture is supported by a pattern that seemingly proves the rule: tropical islands with similar abiotic environments, but greatly reduced biotic diversity, are highly invasible (e.g. Hawaii and the West Indies; Lever, 1985, 1987).

## Native diversity and the invasibility of 'islands'

It is a well-established fact that islands and other insular environments are highly susceptible to invasion. For example, the human-imported plant species that have naturalized on several oceanic islands, including New Zealand and Hawaii, have approximately doubled the sizes of these floras (e.g. Webb *et al.*, 1988; Wagner *et al.*, 1999). The Auckland islands now support an avifauna consisting of nine exotics and 11 natives (Case, 1996). Similar patterns hold for other habitats that are characterized by reduced areas and/or historical isolation. For example, isolated watersheds and river systems in western North America, such as the Sacramento, San Juaquin and Colorado, support more species of exotic than of native fishes (Gido & Brown, 1999). A common feature of these insular habitats owing to their small size and historical isolation is that they support a low diversity of well-differentiated indigenous species. These environments and their biotas are differentially susceptible to colonization by species that have evolved on large land masses with diverse biotas.

We can suggest three reasons why this pattern exists. For the first, assume that, compared to continents, islands offer a similar spectrum of resources and/or habitats. If the continental and insular species are equally specialized, but islands have fewer total species, it necessarily follows that there are no specialists for certain insular resources and/or habitats. This provides the opportunity for specialists, which can utilize these unexploited resources, to invade. For the second reason, make the same assumptions that islands have a similar spectrum of environments and fewer species than continents. If the insular species collectively exploit the entire range of resources and habitats, then it necessarily follows that they are on average more generalized (broader niched) than their continental counterparts. This

also provides the opportunity for specialists, which can more effectively exploit particular resources, to invade. Both of the above alternatives assume, however, that a trade-off exists between the capacity to exploit a particular resource and the spectrum of resources that can be utilized.

A third explanation, rather than assuming a trade-off between specialists and generalists, would suggest that generalized species of continental origins are superior to specialized insular endemics. The positive correlation between abundance and distribution observed in many functional and taxonomic groups implies that those species that can use a broad spectrum of resources are also the dominant consumers of most resource types (Hanski, 1982; Brown, 1984; Gaston & Lawton, 1988, 1990). The same attributes that enable these species to be dominant in most environments within their native range should also allow them to find environments where they can establish and dominate as colonists. Furthermore, because they are abundant and widespread, such species are more likely to be dispersed than those that are rare and narrowly distributed.

This third explanation implies that the dominant species on continents are inherently superior, both to the other species on continents and to the species that they encounter when they invade islands with lower diversity. It also implies that abundant, widely distributed continental species have been tested, and have demonstrated their ability to tolerate a wide range of abiotic conditions, use a broad spectrum of resources, and resist a large number of potential enemies. These species can be likened to Olympic athletes of large nations with well-supported sports programmes; they tend to be superior performers, because they have been drawn selectively from a large pool of individuals and tested in rigorous training regimes. Athletes from Russia, China and the United States win more Olympic medals than those from Jamaica, Lichtenstein and New Zealand.

The inherent superiority of invaders from diverse continental biotas provides a force that can explain insular taxon cycles. Wilson (1961; see also Ricklefs & Cox, 1972, 1978; Roughgarden, 1983; Rummel & Roughgarden, 1985) postulated that the development of insular biotas often exhibits a particular temporal sequence: a spe-

cies from a larger region with a higher species diversity is able to colonize an island; it initially becomes widespread and abundant, but as it evolves becomes progressively rarer and more restricted, and eventually becomes extinct. The generality of these taxon cycles can be questioned (e.g. Whittaker, 1998). However, to the extent that they occur, they exemplify a paradox of invasion: why are the endemic, locally adapted species unable to resist invaders, and why do the invaders in turn ultimately become susceptible to invasion and subsequent replacement? Following dispersal to an island, those species that are abundant, widespread continental ones will often become established in one or more habitats. During their subsequent evolution in the restricted area and low diversity of islands, these species apparently lose the attributes responsible for their initial success, allowing another wave of colonists to invade. The key element in this cycle, then, is the subsequent reduction in fitness of initially superior invaders. Such reduced fitness may occur because selective pressures to invade and improve performance in additional habitats compromises performance in the initially colonized habitats, because counter-adaptations by native species reduce the fitness of colonists, or because of inbreeding and loss of genetic variability in small insular populations (e.g. Nei *et al.*, 1975; Ricklefs & Cox, 1978; Brown & Lomolino, 1998; Whittaker, 1998). Thus, we can understand why invaders of islands embark on an evolutionary trajectory that leads ultimately to extinction and replacement by another wave of colonists.

## Why large continents are invasible

The arguments presented above can account for most cases of invasion. Pre-adaptation to human-modified environments, and escape from coevolved enemies, may account for many invasions of continents, and the evolutionary dynamics of insular species may explain the invasibility of islands. These processes do not seem to be adequate, however, to explain all cases of invasions, especially some examples of invasion of undisturbed continental habitats by species from other large continents. Possible examples include the naturalization of cheat grass, *B. tectorum*, and feral pigs, *Sus scrofa* L., in western North

America. The success of such invaders appears to be due to unique combinations of traits not possessed by any native species. The question, then, is why have no native species evolved an identical or similar suite of traits that permits such success?

The answer, we believe, lies in the imperfect and historically contingent nature of evolution by natural selection. Natural selection tends to maximize fitness by the differential propagation of heritable variance. However, natural selection can only operate on existing variation, and that variation is necessarily limited. Variation comes ultimately from mutation, and because populations and genomes are finite, the number of variants is necessarily limited. Natural selection acting on larger populations can, on average, draw upon a wider range of variation. Furthermore, variants do not arise *de novo*, but are formed by modifications of traits present in ancestors. Because of the finite size of populations and the historical contingency of evolution, it is extremely unlikely, if not absolutely impossible, for natural selection to access the variation required to produce combinations of traits that represent optimal solutions to all environmental challenges. Jacob (1977) has likened natural selection to a tinkerer, who uses the limited available materials to produce workable, but not absolutely optimal, solutions rather than to an engineer, who can design optimal solutions. A related idea is Wright's (1932, 1988) concept of adaptive landscapes. While natural selection tends to increase fitness, it is limited to solutions that can be accessed through existing variation. Adaptive changes tend to find local peaks in the fitness landscape, but are unlikely to find global optima that would require crossing valleys in the landscape.

The implication, then, is that evolution by natural selection is imperfect and native species do not necessarily possess the suites of traits that represent optimal adaptations to local conditions. There is some probability that organisms that have evolved in some other place may possess a superior combination of attributes. The probability of an alien species having a combination of traits that is superior to any native species is obviously much higher on small isolated islands, which necessarily sample much less variation, than on large con-

tinents with large populations and high species diversity. Nevertheless, continental biotas are also susceptible to invasion, because there is some probability that alien species have combinations of traits that are superior to those of any natives.

## CONCLUSIONS

Ultimately, of course, there is no paradox of invasion. Those features of invading species and invaded environments that initially appeared to be paradoxical must ultimately have some mechanistic explanation. We have focused on two phenomena that are not easily explained: (1) most invasions, even those that are ultimately successful, fail; and (2) despite the fact that they have not had the opportunity to adapt to the local environment, some invaders are able to establish, and sometimes to dominate and even to replace native species. Some explanations for these phenomena are well established in the literature: demographic and environmental stochasticity, adaptations to novel human-altered environments and release from enemies. We focus on additional mechanisms: environmental variation over space, the role of dispersal in metapopulation dynamics, the superior qualities of colonists from large species-rich regions and the historical contingency of evolution. Consequently, invasion is not paradoxical. In fact, the initial establishment and ultimate success of alien species in invading locally adapted endemic biotas can be explained readily in terms of known ecological and evolutionary processes.

## ACKNOWLEDGMENTS

## REFERENCES

Baker, H.G. (1965) Characteristics and modes of origin of weeds. *The genetics of colonizing*

*species* (ed. by H.G. Baker & G.L. Stebbins), pp. 147–168. Academic Press, New York.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.

Brown, J.H. (1989) Patterns, modes and extents of invasions by vertebrates. *Biological invasions, a global perspective* (ed. by J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek & M. Williamson), pp. 85–109. Wiley, New York.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography, effect of immigration on extinction. *Ecology*, **58**, 445–449.

Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer Press, Sunderland, MA.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range, size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597–623.

Brown, N.S. & Wilson, G.I. (1975) A comparison of the ectoparasites of the house sparrow (*Passer domesticus*) from North America and Europe. *American Midland Naturalist*, **94**, 154–165.

Burke, M.J.W. & Grime, J.P. (1996) An experimental study of plant community invasibility. *Ecology*, **77**, 776–790.

Carlquist, S. (1965) *Island life, a natural history of the islands of the world*. Natural History Press, Garden City, New York.

Carlquist, S. (1974) *Island biology*. Columbia University Press, New York.

Carlton, J.T. (1979) Introduced invertebrates of San Francisco Bay. *San Francisco Bay, the urbanized estuary* (ed. by T.J. Conomos), pp. 427–444. American Association for the Advancement of Science, Pacific Division, San Francisco.

Case, T.J. (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Science USA*, **87**, 9610–9614.

Case, T.J. (1996) Global patterns in the establishment and distribution of exotic birds. *Biological Conservation*, **78**, 69–96.

Clarke, C.M.H. (1971) Liberations and dispersal of red deer in northern South Island districts. *New Zealand Journal of Forest Science*, **1**, 194–207.

Crawley, M.J. (1987) What makes a community invasible? Colonization, succession, and stability. *The 26th Symposium of the British Ecological Society Held Jointly with the Linnean Society of London* (ed. by A.J. Gray, M.J. Crawley & P.J. Edwards), pp. 429–453. Blackwell Scientific Publications, Oxford.

D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.

Darwin, C. (1859) *On the origin of species*. Murray, London.

Dodd, A.P. (1959) The biological control of prickly pear in Australia. *Biogeography and ecology in Australia, Monographiae Biologicae 8* (ed. by A.E.M. Nairn), pp. 565–577. Dr W. Junk BV, The Hague, The Netherlands.

Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M. & Williamson, M., eds (1989) *Biological invasions, a global perspective*. John Wiley and Sons, New York.

Ebenhard, T. (1988) Introduced birds and mammals and their ecological effects. *Swedish Wildlife Research*, **13**, 1–107.

Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen and Co, London.

Fenner, F. & Ratcliffe, F.N. (1965) *Myxomatosis*. Cambridge University Press, Cambridge.

Forcella, F. & Wood, J.T. (1984) Colonization potential of alien weeds are related to their 'native' distributions, implications for plant quarantine. *Journal of the Australian Institute of Agricultural Science*, **50**, 35–41.

Fox, M.D. & Fox, B.J. (1986) The susceptibility of natural communities to invasion. *Ecology of biological invasions* (ed. by R.H. Groves & J.J. Burdon), pp. 57–66. Cambridge University Press, Cambridge.

Frankell, R.E. (1977) Ruderal vegetation along some Californian roadsides. *University of California Publications in Geography*, **20**, 1–163.

Fritts, T.H. & Rodda, G.H. (1998) The role of introduced species in the degradation of island ecosystems, a case history of Guam. *Annual Review of Ecology and Systematics*, **29**, 113–140.

Gaston, K.J. & Lawton, J.H. (1988) Patterns in the distribution and abundance of insect populations. *Nature*, **331**, 709–712.

Gaston, K.J. & Lawton, J.H. (1990) Effects of scale on the relationship between regional distribution and local abundance. *Oikos*, **58**, 329–335.

Gido, K.B. & Brown, J.H. (1999) Invasion of North American drainages by alien fish species. *Freshwater Biology*, **42**, 387–399.

Gilpin, M.E. & Soulé, M.E. (1986) Minimum viable populations, processes of species extinction. *Conservation biology, the science of scarcity and diversity* (ed. by M.E. Soulé), pp. 19–34. Sinauer, Sunderland, MA.

Grinnell, J. (1922) The role of the 'accidental'. *The Auk*, **39**, 373–380.

Hair, J.D. & Forrester, D.J. (1970) The helminth parasites of the starling (*Sturnus vulgaris* L.), a checklist and analysis. *American Midland Naturalist*, **83**, 555–564.

Hanski, I. (1982) Dynamics of regional distribution, the core and satellite species hypothesis. *Oikos*, **38**, 210–221.

Harris, P., Peschken, D. & Milroy, J. (1969) The status of biological control of the weed *Hypericum perforatum* in British Columbia. *Canadian Entomologist*, **101**, 1–15.

Hengeveld, R. (1989) *Dynamics of biological invasions*. Chapman & Hall, New York.

Huffaker, C.B. & Kennett, C.E. (1959) A ten-year study of vegetational changes associated with biological control of Klamath weed. *Journal of Range Management*, **12**, 69–82.

Jacob, F. (1977) Evolution and tinkering. *Science*, **196**, 1161–1166.

Lack, D. (1970) Island birds. *Biotropica*, **2**, 29–31.

Lande, R. (1988) Genetics and demography in biological conservation. *Science*, **241**, 1455–1460.

Lever, C. (1985) *Naturalized mammals of the world*. Longman, Essex, UK.

Lever, C. (1987) *Naturalized birds of the world*. Longman, Essex, UK.

Mack, R.N. (1981) Invasion of *Bromus tectorum* L. into western North America, an ecological chronicle. *Agro-Ecosystems*, **7**, 145–165.

Mack, R.N. (1995) Understanding the process of weed invasions, the influence of environmental stochasticity. *Weeds in a changing world, BCPC Symposium Proceedings Number 64*, British Crop Protection Council, UK.

Moulton, M.P. & Pimm, S.L. (1986) Species introductions to Hawaii. *Ecology of biological invasions of North America and Hawaii* (ed. by H.A. Mooney & J.A. Drake), pp. 231–249. Springer-Verlag, New York.

Murdoch, W.W., Chesson, J. & Chesson, P.L. (1985) Biological control in theory and practice. *American Naturalist*, **125**, 344–366.

Nei, M., Maruyama, T. & Chakraborty, R. (1975) The bottleneck effect and genetic variability in populations. *Evolution*, **29**, 1–10.

Newsome, A.E. & Noble, I.R. (1986) Ecological and physiological characters of invading species. *Ecology of biological invasions* (ed. by R.H. Groves & J.J. Burdon), pp. 1–20. Cambridge University Press, Cambridge.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.

Rejmánek, M. (1996) A theory of seed plant invasiveness, the first sketch. *Biological Conservation*, **78**, 171–181.

Ricklefs, R.E. & Cox, G.W. (1972) Taxon cycle in the west Indian avifauna. *American Naturalist*, **106**, 195–219.

Ricklefs, R.E. & Cox, G.W. (1978) Stage of taxon cycle, habitat distribution, and population density in the avifauna of the West Indies. *American Naturalist*, **112**, 875–895.

Roughgarden, J. (1983) Coevolution between competitors. *Coevolution* (ed. by D.J. Futuyma & M.S. Slatkin), pp. 388–403. Sinauer Associates, Sunderland, MA.

Rummel, J.D. & Roughgarden, J. (1985) A theory of faunal buildup for competition communities. *Evolution*, **39**, 1009–1033.

Schierenbeck, K.A., Mack, R.N. & Sharitz, R.R. (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology*, **75**, 1661–1672.

Shaffer, M.L. (1981) Minimum population sizes for species conservation. *Bioscience*, **31**, 131–134.

Shaffer, M.L. (1987) Minimum viable populations, coping with uncertainty. *Viable populations for conservation* (ed. by M.E. Soulé), pp. 69–86. Cambridge University Press, Cambridge.

Shmida, A. & Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1–20.

Simberloff, D. (1988) The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics*, **19**, 473–511.

Stebbins, G.L. (1965) Colonizing species of the native California flora. *The genetics of colonizing species* (ed. by H.G. Baker & G.L. Stebbins), pp. 173–191. Academic Press, New York.

Suarez, A.V., Bolger, D.T. & Case, T.J. (1998) Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology*, **79**, 2041–2056.

Veltman, C.J., Nee, S. & Crawley, M.J. (1996) Correlates of introduction success in exotic New Zealand birds. *American Naturalist*, **147**, 542–557.

Vitousek, P.M., Walker, L.R., Witeaker, L.D., Mueller-Dombois, D. & Matson, P.A. (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science*, **238**, 802–804.

Vitousek, P.M. & Walker, L.R. (1989) Biological invasion by *Myrica faya* in Hawaii, plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs*, **59**, 247–265.

Vivrette, N.J. & Muller, C.H. (1977) Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. *Ecological Monographs*, **47**, 301–318.

Wagner, W.L., Herbst, D.R. & Sohmer, S.H. (1999) *Manual of flowering plants of Hawai'i*, revised edn. University of Hawai'i Press, Honolulu.

Wallace, A.R. (1880) *Island life, or the phenomena and causes of insular faunas and floras, including a revision and attempted solution of the problem of geological climates*. Macmillan Press, London.

Webb, C.J., Sykes, W.R. & Garnock-Jones, P.J. (1988) *Flora of New Zealand*, Vol. 4, *Naturalized Pteridophytes, Gymnosperms, Dicotyledons*. Singapore National Printers Ltd, Singapore.

Whittaker, R.J. (1998) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.

Williamson, M. (1981) *Island populations*. Oxford University Press, Oxford.

Williamson, M. (1996) *Biological invasions*. Chapman & Hall, London.

Wilson, E.O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist*, **95**, 169–193.

Wright, S. (1932) The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proceedings of the XI International Congress of Genetics*, **1**, 356–366.

Wright, S. (1988) Surfaces of selective value revisited. *American Naturalist*, **131**, 115–123.