

Chapter 18

Success factors in the establishment of human-dispersed organisms

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Introduction

As recently as a decade ago, exotic organisms—species dispersed beyond their native ranges by human activities—rarely ranked high among recognized threats to biodiversity. Habitat loss and habitat alteration, including global climate change, usually headed lists of such threats. Pollution was also placed high, along with hunting and fishing, including the hunting of whales and fur seals, the harvesting of animal tusks and organs for ornament or medicine, the taking of sea turtles and coral reef fish, and the death of dolphins entangled in tuna nets. Exotic species were generally placed near the bottom, if indeed they were on the list at all. But perceptions are changing.

In 10 recent assessments of threats to different groups of organisms, most studies concluded that exotic species are a leading threat to biodiversity (Table 18.1). For example, Wilcove *et al.* (1998) found that competition with, or predation by, exotic species constituted the second greatest threat to imperiled plants and animals in the United States, second to habitat loss or degradation, but affecting more than twice as many imperiled species as pollution, and nearly three times as many species as over-exploitation. In 1998, the World Conservation Union ranked exotic species as the second greatest threat to biodiversity, after habitat loss (Raver 1999); and in 2000, the Director of the US Geological Survey predicted that the spread of invasive organisms would be the second most serious ecological problem facing the United States in the 21st century (Groat 2000).

Besides affecting biodiversity, the introduction of exotic organisms can have substantial economic, social and public health impacts—and we live in a world today in which those impacts are likely to grow. Unless countermeasures are taken, a massive increase in the rapid transport and release of organisms around the world is a predictable consequence of the current expansion in international trade. As new global markets are developed, organisms are moved both intentionally and accidentally along a growing number of pathways, between a changing array of source regions and destinations, via an alarming diversity of mechanisms. Among marine species, for example, organisms are transported between and across oceans as plankton in

Table 18.1 Ranking of factors in the imperilment, endangerment or extinction of species. 'ESA-listed' taxa are species, subspecies or vertebrate populations listed as threatened or endangered under the US Endangered Species Act.

Assessment	Ranking of exotic species	Reference
Factors contributing to the loss of the 40 recently extinct North American fish species and subspecies	2nd most frequent of 5 factors	Miller <i>et al.</i> 1989
Threats to the 364 imperiled North American fish species and subspecies. Exotic species included in one category in combination with hybridization, predation and competition	2nd most frequent of 4 categories of threats	Williams <i>et al.</i> 1989
Primary causes of endangerment for 98 ESA-listed plant species	Tied for 8th most frequent of 14 causes	Schemske <i>et al.</i> 1994
Primary threats to 1111 imperiled bird species worldwide	4th most frequent threat	Collar <i>et al.</i> 1994
General factors adversely affecting 667 ESA-listed species. Exotic species included in an 'interspecific interactions' factor, defined to include disease, predation and competition, particularly as associated with exotic species	2nd most frequent of 5 factors	Flather <i>et al.</i> 1994
Specific reasons contributing to the endangerment of 667 ESA-listed species (among reasons affecting at least 15% of species)	2nd most frequent of 18 reasons	Flather <i>et al.</i> 1994
Factors cited in listings of 68 ESA-listed fish	2nd most frequent of 3 factors	Lassuy 1995
Sources of stressors cited by biologists as causing historic declines in 135 imperiled species in the USA	4th most common of 20 sources	Richter <i>et al.</i> 1997
Sources of stressors cited by biologists as limiting recovery in 135 imperiled species in the USA	3rd most common of 20 sources	Richter <i>et al.</i> 1997
Factors contributing to the imperilment of 1880 taxa of plants and animals in the USA	2nd most frequent of 5 factors	Wilcove <i>et al.</i> 1998

the ballast tanks and seawater piping systems of cargo vessels, as sedentary organisms attached to the hulls of boats and ships, as breeding stock and food for aquaculture, as goods in the saltwater aquarium, live seafood and live bait trades, and as endozoic, epizotic or otherwise associated biota inadvertently shipped with any of these. Terrestrial and freshwater species are transported by a similarly diverse set of vectors. These globe-trotting species will inevitably include some organisms that substantially alter native ecosystems on land and in the sea; pests of forests, crops and livestock; and human parasites and diseases, including emergent diseases and antibiotic-resistant strains of diseases that had been thought to be under control.

There has thus been much interest in understanding which traits of organisms make them more or less successful as invaders, and which characteristics of habitats make them more or less vulnerable to invasions. Charles Elton, for example, in *The Ecology of Invasions by Animals and Plants* (1958), noted that 'invasions most often come to cultivated land, or land much modified by human practice,' or to more natural areas that none the less 'have also suffered the results of human occupation.' He also suggested that islands were especially heavily invaded, devoting an entire

chapter to island invasions. In a 1964 symposium on the genetics of colonizing species, organized by Herbert Baker and Ledyard Stebbins, the genetic, reproductive and life-history traits of successful invaders were frequent points of discussion. In his own presentation, Baker (1965a) compared congeneric pairs of plant species, one of which had spread widely and the other of which had not; and in an appendix to his talk provided an oft-cited list of the traits of the 'ideal weed'.

In the 1980s, the Scientific Committee on Problems of the Environment (SCOPE) of the International Council of Scientific Unions supported an extensive programme of enquiry into biological invasions, which focused on the questions of what makes a species a successful invader and what makes a site prone to invasion. The programme sponsored several international symposia that resulted in a series of publications described by Mooney and Drake (1989) and Williamson (1996). Contributions to these publications, and other papers published in the scientific literature, have suggested a bewilderingly large number of traits as being typical of successfully invading species, including such possibly contradictory traits as plant seeds being, on the one hand, large (Baker 1965b; Mayr 1965b), or, on the other hand, small (Rejmanek & Richardson 1996) and numerous (Mulligan 1965; Groves 1986; Pimental 1986); a lifespan that is short (Orians 1986; Di Castri 1990) or long (Crawley 1986; Möller 1996; Townsend 1996); and a body size that is small (Crawley 1986, 1987; Di Castri 1990) or large (Ehrlich 1986, 1989; Möller 1996; Townsend 1996).

Compelling data that either support or refute the various characteristics proposed for successful invaders or vulnerable environments have been difficult to come by, leading some workers to suggest that the search for broad, predictive characteristics may be futile (Simberloff 1986, 1989; Williamson 1996). Nevertheless, that certain traits do generally contribute to the success of invasions has been widely accepted by many researchers and resource managers, and used in some risk assessment protocols for invasions (Ruesink *et al.* 1995). Some of the most frequently cited generalizations are that organisms that invade successfully are opportunistic, 'r-selected' species with a high reproductive output and wide environmental tolerances, are generalists in resource use, and have escaped from their natural predators or parasites in their new environment; and that islands, disturbed habitats and species-poor communities are particularly vulnerable to invasions. These propositions generally have their roots in the idea that the success or failure of invasions is governed by biotic interactions between the invading and resident species—that is, that species with these traits are in some broad sense better competitors than species lacking them, and that the more vulnerable types of environments host fewer or weaker competitors and predators.

In this chapter, I will examine the evidence for four of these propositions: (i) that islands are particularly vulnerable to invasions; (ii) that disturbed habitats are particularly vulnerable to invasions; (iii) that organisms that produce large numbers of young are more successful as invaders; and (iv) that organisms frequently succeed as invaders because they have left their native parasites behind. Specifically, I will ask whether there is evidence to support a conclusion that these characteristics increase

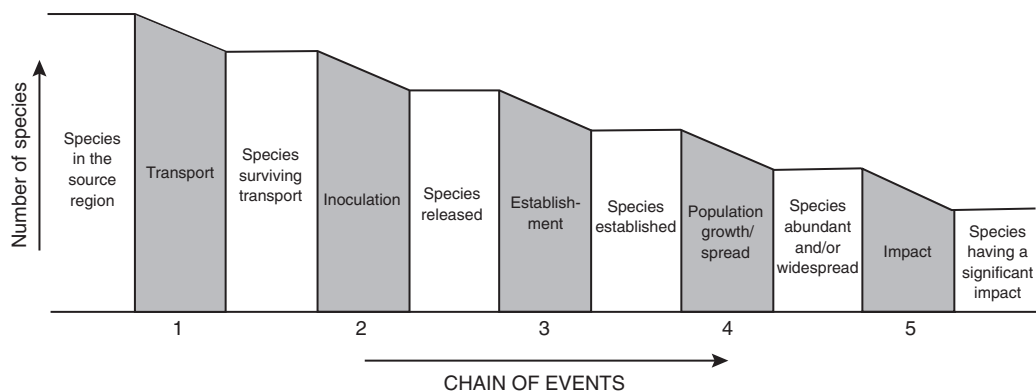


Figure 18.1 An invasion conceived as stages separated by steps or ‘filters’.

the probability that a species released into a novel environment will become established there. First, however, I will refer to a conceptual model of invasions to define some of the terms of this enquiry, and discuss the types of evidence and analyses that have been offered in regard to these propositions.

A conceptual model of invasions

Figure 18.1 provides a visual model of invasions, similar to models proposed by other workers. An invasion is shown as a series of stages characterized by progressively shrinking sets of species—the species present in the source region, the smaller set of species that survive transport to the new region, and so on. Between these stages are steps or processes, distinguished by a grey background and numbered for discussion, labelled ‘transport’, ‘inoculation’, etc. It is helpful to think of these steps as filters, and our questions may then be framed as asking what species’ traits make it more likely that a species will pass through one or other filter or group of filters, and what environmental characteristics make it more likely that a larger number of species will pass through.

Different researchers have been concerned in their investigations with different filters, and unfortunately, due to ambiguities in terminology or in the way they have presented their results, it has not always been clear to which filters their work refers. The main value of a model like this is that it allows us to discuss this without ambiguity, or at least with less ambiguity, even where different terminology has been used. Thus Williamson and Fitter (1996a, 1996b) and Williamson (1996) discuss patterns in the percentage of organisms that pass the second filter (here called ‘inoculation’, but which they call ‘escaping’), the third filter (as here, called ‘establishing’) and the fourth and fifth filters (‘becoming a pest’). Some research on invasion success has addressed other filters or combinations, such as which established organisms will spread in a new environment (the fourth filter), or which of the organisms released into an environment are likely to have an impact there (the third through fifth

filters), or which of the organisms present in a region are likely to spread to other regions (the first through third filters).

In the general view, particular characteristics of species or environments have usually been perceived as either promoting or inhibiting the invasion process as a whole, without considering the potential for different effects at different stages of invasion. Characteristics associated with passage through one filter may differ from those associated with passage through another, and a characteristic that assists passage through one filter may even retard passage through another. For example, Crawley (1986) found that among insects released to control weeds, egg dispersal and a long lifespan generally correlated with the likelihood of establishment (the third filter), while egg aggregation and a short lifespan generally correlated with the degree of control (the fourth and fifth filters).

In a recent review, Kolar and Lodge (2001) considered studies published in the scientific literature between 1986 and 1999 with reference to an invasion model with three steps or 'transitions': transport and introduction (corresponding to the first two filters), establishment (the third filter) and invasion (defined as becoming widespread, the fourth filter). They looked for studies that included at least 20 species and that quantitatively analysed whether species' traits other than taxonomic identity were associated with success or failure in passing through these transitions in the field. They found only one study that addressed the transport and introduction transition, and 14 studies that addressed the establishment or invasion transitions. Among these, analyses of the establishment transition were primarily conducted on birds, and analyses of the invasion transition were primarily conducted on plants.

In this chapter I will be focusing on the third filter, seeking quantitative analyses of success and failure in the field that indicate whether certain species' traits and habitat characteristics assist or prevent the establishment of species released into novel environments. Consistent with Kolar and Lodge (2001), the relevant analyses that I found were limited to animal data.

Approaches to analysing the effect of species and environmental traits on invasion success

Species' traits said to contribute to the success of invasions have often been identified on the basis of those traits being common in species that had passed through the filter or filters of interest, such as traits common in species that had spread to new regions, or that had caused problems in new regions, etc. But, as others have pointed out (e.g. Crawley 1986; Simberloff 1986, 1989, 1995), drawing meaningful conclusions about the effect of these traits requires information about both the successful and the unsuccessful invaders (i.e. what was poured into the filters), not just about the successful invaders (what passed through the filters). Similarly, determining the role played by environmental characteristics requires knowledge of the rates of success and failure in environments displaying and lacking the characteristics of interest. In a few, but very few, cases, this sort of knowledge has been compiled and

analysed. With regard to the ability of exotic organisms inoculated into an environment to become established there, such analyses have been primarily conducted on biocontrol agents (primarily arthropods; e.g. Hall & Ehler 1979; Crawley 1986, 1987; Simberloff 1986), released and escaped birds (e.g. Moulton & Pimm 1986; Newsome & Noble 1986; Pimm 1989; Simberloff & Boecklen 1991; Lockwood *et al.* 1993; Moulton 1993; Lockwood & Moulton 1994; Brooke *et al.* 1995; Case 1996; Veltman *et al.* 1996; Duncan 1997; Green 1997) and intentionally released fish (Cohen 1996). But in most cases other than intentional releases, and in many circumstances where intentional releases were poorly documented, we know little about which organisms were released into the environment but failed to establish.

Accordingly, some researchers have turned to proxy data sets of species, on the sometimes unstated assumption that the distribution of traits in the proxy set is the same as the distribution of traits in the set of species released. A frequent practice has been to use the native species in a region as a proxy for the species released into the region (e.g. Mulligan 1965 using Canadian plants; Crawley 1986 using British birds and mammals; Crawley 1987 using northeastern USA plants). But without any *a priori* reason for believing that the traits of the proxy set and the traits of the set of released species are the same, such analyses are suspect.

That certain traits contribute generally to invasion success has also been argued on theoretical grounds (e.g. Pimm 1989, based on community assembly and food web models). Of course, however useful such arguments are for framing hypotheses, they cannot inform us about what is really going on in the world. Physical models consisting of artificial ecosystems (primarily aquatic microcosms, e.g. Robinson & Dickerson 1984) and field experiments (usually manipulating plots of terrestrial plants, e.g. Tilman 1997; other studies referenced in Hobbs & Huenneke 1992; and Stohlgren *et al.* 1999) have also been used to test for species' traits or environmental characteristics that influence invasion success. Some observers commend the field experimental approach as the best hope for progress toward understanding what affects the potential for successful invasions (Kareiva 1996; Mack 1996). But unless corroborated by analyses of invasions in real ecosystems, the relevance of studies in micocosms or manipulated plots remains uncertain.

Are islands especially vulnerable to invasions?

The large number of exotic species established on islands is impressive, in many cases accounting for a substantial portion of the island biota (e.g. Sailer 1978; Simberloff 1986; Atkinson 1989). This has encouraged a long-held belief that islands are more easily invaded than continents, which is also partly based on a perception that island species are in general weaker competitors, less aggressive predators and more poorly defended than mainland species, and that island communities as a whole are more fragile and characterized by less intensive competition than mainland communities (Elton 1958; Carlquist 1965; Mayr 1965a; Simberloff 1986, 1989, 1995; Loope & Mueller-Dombois 1989; Bowen & van Vuren 1997). This is summed up in the concept of 'biotic resistance', a term invoking the tendency to exclude

Table 18.2 Establishment of biocontrol arthropods on islands and continents. (Adapted from Hall & Ehler 1979; based on worldwide data from Clausen 1978.)

Habitat	<i>n</i>	Rate of establishment	χ^2	<i>P</i>
Continents	1468	0.30	21.96	<0.0005
Islands	827	0.40		

organisms either by competition or by attack from predators or parasites (Simberloff 1985, 1989, 1995). Islands are said to offer less biotic resistance than continents.

A somewhat different explanation for the presumed greater invasibility of islands is that they contain what is generally described as numerous vacant niches (however unpalatable that term is to some researchers) (Herbold & Moyle 1986) relative to mainland ecosystems, and thus more opportunities for exotic species to establish without encountering any direct competition (Loope & Mueller-Dombois 1989; Simberloff 1995). Simberloff (1986) argued further that because of the smaller number of native species on islands, the filling of each new niche would represent a proportionally greater habitat change on islands than on continents, and thus a proportionally greater creation of new niches for yet additional species to invade. Thus, the establishment of a few exotic plants on an island with an impoverished flora would provide a substantially greater proportion of new habitat for phytophagous insects than would the same level of exotic plant establishment on a continent, and the establishment of a few species of exotic vertebrates on an island with a poor vertebrate fauna would create relatively more new niches for vertebrate parasites (Simberloff 1986).

These ideas have been much debated, as reviewed by Simberloff (1986, 1989, 1995). Several researchers have drawn conclusions about the relative invasibility of islands and continents based on the numbers of exotic species or the proportion of the biota consisting of exotic species in these habitats (e.g. Imms 1931; DeBach 1965; Sailer 1978). However, there have been few analyses comparing the rates of successful establishment of organisms released on islands and continents. In one, Hall and Ehler (1979) analysed global data from Clausen (1978) on arthropods used to control insects and arachnids, and found that the released organisms were more successful at establishing on islands than on continents (Table 18.2).

Simberloff (1986) argued that the organisms used for analysis should be related, to avoid possible confounding factors. He selected for analysis from the records in Clausen (1978) the six insect genera with the largest number of species that had been moved among islands and continents, each with about 20 species recorded. His analysis addressed together the two hypotheses that: (A) continents are more resistant to invasions than islands, and (B) continental species are more successful at invading than island species, by looking at the relative rates of establishment in four types of releases:

- 1 Continental species released on islands (should have the highest rate of establishment if hypotheses A and B are true).
- 2 Continental species released on continents (should have an intermediate rate of establishment).
- 3 Island species released on islands (should also have an intermediate rate of establishment).
- 4 Island species released on continents (should have the lowest rate of establishment).

Of the four genera for which there were adequate data to conduct an analysis, two (*Aphytis* and *Bracon*) generally fitted the above pattern and two did not (Table 18.3). When data for the six genera were pooled, the data fitted the pattern but the differences were not significant. Reviewing this and other evidence (though apparently not including Hall and Ehler's (1979) analysis), Simberloff (1989) found that although the data were insufficient to draw strong conclusions, it appeared likely to him that islands are more vulnerable to invasion than continents.

The data used by Simberloff can also be assessed directly for differences in rates of establishment on islands and continents. When releases of the continental and island species in a genus are considered separately (to avoid the possibility of confounding differences between island and continental species in their ability to establish), there is a higher rate of establishment on islands than on continents in six of the seven cases where there are data (Table 18.3). However, in only one of the six cases of greater establishment on islands is the difference significant (the release of continental species of *Opius*: $\chi^2 = 6.277$, $P = 0.0122$).

Newsome and Noble (1986) analysed the birds released in Australia relative to establishment in island and mainland regions. They included releases of both foreign birds and of translocated Australian birds and included Tasmania as part of the mainland, and found a non-significant higher rate of establishment on the islands. When they removed Kangaroo Island, the largest island, from the analysis, the difference became significant (Table 18.4).

Case (1996) assembled data on the numbers of successful and failed bird introductions in 22 islands and regions within continents. For analysis, he took the residuals from a regression of the number of successful introductions on the number of failed introductions at each site, which he described as a measure of the relative success rate, and used them as the dependent variable in a stepwise regression with various candidate independent variables, including the areas of the regions. The areas were not significantly correlated with relative success rate. Table 18.5 lists Case's (1996) data on the rates of establishment of exotic birds, along with data from a few other sources. Areas are included to allow sorting into islands and continents for analysis. A pattern of increasing rate of establishment with decreasing area seems clear, but as these data were assembled by different researchers for different time periods using different methods or definitions to determine the number of species introduced and established, it seems unwise to attempt a statistical analysis. Instead I analysed Case's data by sorting the regions into continent and island groups, counting all successful and unsuccessful introductions of a species into a region, and

Table 18.3 Rates of establishment in insect genera widely deployed for biocontrol. (Adapted from Simberloff 1986.)

	Continental species released on				Island species released on			
	Islands		Continents		Islands		Continents	
	<i>n</i>	Rate of establishment	<i>n</i>	Rate of establishment	<i>n</i>	Rate of establishment	<i>n</i>	Rate of establishment
<i>Opius</i>	24	0.46	37	0.14	6	0.67	6	0.50
<i>Aphytis</i>	16	0.69	48	0.67	0	No data	2	0.50
<i>Bracon</i>	11	0.36	28	0.14	6	0.33	2	0.00
<i>Apanteles</i>	11	0.73	27	0.59	5	0.40	1	1.00
Six genera of insects	71	0.49	176	0.43	19	0.47	15	0.33

Table 18.4 Rates of establishment of birds in Australia, including both foreign species and translocated native species. (Adapted from Newsome & Noble 1986.)

Habitat	<i>n</i>	Rate of establishment	χ^2	<i>P</i>
Including Kangaroo Island				
Mainland (Australia and Tasmania)	72	0.47	2.52	ns
Islands	65	0.63		
Excluding Kangaroo Island				
Mainland (Australia and Tasmania)	72	0.47	6.45	<0.05
Islands	52	0.73		

ns, not significant.

Table 18.5 Rates of establishment of birds. For the larger regions the area given is for the entire continent or archipelago (i.e. British Isles, Australia and North America), though the establishment rates refer to parts of these.

Invaded area	Rate of establishment	Area of island or continent (km ²)	Reference
Lord Howe	0.69–0.75	13	Mayr 1965a; Case 1996
Norfolk	0.92	40	Case 1996
Bermuda	0.41–0.88	54	Mayr 1965a; Case 1996
Chagos Archipelago	0.58	65	Case 1996
Ascension	0.29	90	Case 1996
Rodriguez	0.64	109	Case 1996
Saint Helena	0.31	125	Case 1996
Seychelles (granitic)	0.67	233	Case 1996
Tahiti	0.20	1041	Case 1996
Hawaii (non-mongoose)	0.52	1422	Case 1996
Mauritius	0.43	1865	Case 1996
Comoros	0.50	1958	Case 1996
Fiji (non-mongoose)	0.39	2375	Case 1996
Reunion	0.53	2512	Case 1996
Kangaroo Island	0.58	3890	Case 1996
Hawaii (mongoose)	0.46	12 136	Case 1996
Hawaii (all)	0.48	16 708	Mayr 1965a
Fiji (mongoose)	0.33	15 921	Case 1996
Tasmania	0.81	67 900	Case 1996
New Zealand	0.20–0.30	266 800	Mayr 1965a; Case 1996; Veltman <i>et al.</i> 1996; Green 1997
Great Britain	0.30	312 900	Case 1996
Australia (Victoria)	c.0.20–0.33	7 642 000	Mayr 1965a; Case 1996
Australia (Sydney County)	≤0.30	7 642 000	Mayr 1965a
Australia (including islands)	0.44	7 642 000	Newsome & Noble 1986
Europe	0.15	10 036 000	Mayr 1965a
Continental United States	0.13	24 326 000	Case 1996

Table 18.6 Rates of establishment of birds on continents and islands. (Based on data from Case 1996.)

Continents are defined to include	Continents		Islands		χ^2	<i>P</i>
	<i>n</i>	Rate of establishment	<i>n</i>	Rate of establishment		
North America	98	0.13	743	0.41	27.02	<0.001
North America, Australia	146	0.20	695	0.41	23.01	<0.001
North America, Australia, British Isles	176	0.22	665	0.42	23.71	<0.001
North America, Australia, British Isles, New Zealand	325	0.24	516	0.46	39.49	<0.001
North America, Australia, British Isles, New Zealand, Tasmania	341	0.27	500	0.45	27.27	<0.001

comparing these for the two groups using a 2×2 contingency test. I defined the lower limit of continent size at, successively, the area of North America, of Australia, of the British Isles, of New Zealand, and of Tasmania, so that there are five tests (Table 18.6). The differences were highly significant for all definitions of continent.

There may be some pseudoreplication problems with these data. For example, Case divided the Hawaiian and Fijian island groups by the presence/absence of the mongoose for a different analysis, but Simberloff and Boecklen (1991) argued that for the present sort of analysis observations on different islands within an archipelago are not truly independent observations since birds established on one island may then colonize another. Case also counted established exotic birds for which he had no record of introduction as introduced and established. These probably represent a combination of self-colonizations, cage escapes or intentional but unrecorded releases. Failures from these types of introductions would rarely or never be recorded, so the rates of establishment are probably inflated. If self-colonizations of species from continents to nearby islands are more common than the reverse (which seems likely given that continents have many species that are absent from nearby islands and thus a large pool of potential colonists, while islands rarely have species that are absent from nearby continents), then rates of establishment in these data are probably inflated for islands relative to continents.

Despite these problems, the highly significant results from this analysis of birds and from Hall and Ehler's (1979) analysis of biocontrol releases, and the weak pattern in Simberloff's (1986) analysis of biocontrol releases and Newsome and Noble's (1986) analysis of birds, when taken together strongly suggest that islands are in fact more vulnerable to the establishment of exotic species than continents. Simberloff (1986, 1989, 1995) notes that biocontrol releases are primarily into agricultural communities, which host few native organisms and are more similar to islands and continents than are native communities. Thus any patterns derived from

differences in the characteristics of island and mainland species or the resistance of natural communities would be muted or missing from biocontrol data. Simberloff (1995) argues that the same issue arises with bird data, at least on the Hawaiian and Mascarene islands (but not in Bermuda; Lockwood & Moulton 1994), where exotic birds primarily occupy highly altered, anthropogenous habitat and have limited interactions with native birds. That statistically strong differences in establishment rates between islands and continents can be found in spite of this is striking. If interactions with native biota or native communities on islands and continents are not the cause of these differences, then what is?

Are disturbed habitats more easily invaded?

The idea that invasions are more successful in disturbed than in undisturbed habitats has a long pedigree (e.g. Elton 1958; Mooney & Drake 1989; Hobbs & Huenneke 1992), and is most often attributed to a reduction in the level of competition in disturbed habitats (Ehrlich 1989; Luzon & MacIsaac 1997). Lozon and MacIssac (1997), in a review of 133 studies of invasions published in 10 journals from 1993 to 1995, found that disturbance was associated with the establishment of exotic species by 68% of the papers discussing exotic plants and by 28% of the papers discussing exotic animals. In these papers, 86% of the exotic plants and 12% of the exotic animals studied were reported to be dependent on disturbance for establishment. However, disturbance means different things to different investigators. Hobbs and Huenneke (1992) reviewed definitions ranging from the relatively specific ('a process that removes or damages biomass'—Grime 1979) to the perhaps uselessly broad ('any process that alters the birth and death rates of individuals present in the patch'—Petraitis *et al.* 1989). Others have considered any change from past conditions to be a disturbance. Examples of disturbance cited in these studies include fire, the suppression of fire, flood, drought, irrigation, soil disturbance by animals or mechanical activity, grazing, the removal of grazing, and the release of exotic species. In different studies, a site may be considered disturbed if it is subject to repeated or continuous perturbation; has undergone a change from previous conditions; differs from natural conditions; has a reduced biota, in terms of species or individuals; has reduced plant cover; or has disturbed soils. The flexible meaning of disturbance, combined with the various definitions of invasion discussed above, have given this proposition a particularly amorphous character.

It is none the less apparent that exotic organisms are often common in areas of substantial human activity or alterations, which would be considered to be disturbed environments by several definitions. Exotic organisms are generally more common in areas altered by urban or agricultural development than in pristine areas, more common along roadsides than away from roads, more common in rivers that have been altered by dams than in those that have not, and more common in harbours and estuaries than in open coast or open ocean areas. However, this is not necessarily because areas of human activity and alteration are more vulnerable to invasion. There are at least three other possible explanations.

First, exotic organisms are primarily transported to, and released into, areas with substantial human activity (Simberloff 1986, 1989; Williamson 1996; Cohen & Carlton 1998; Mack *et al.* 2000). Exotic crop and livestock species are purposefully introduced into agricultural regions, bringing with them accidental inoculations of exotic weeds, pests and parasites, which sometimes in turn lead to releases of additional exotic organisms to control the weeds, pests and parasites. People and goods from distant lands, and associated organisms, arrive in urban areas in great numbers. Exotic fish are frequently released in the reservoirs impounded by dams. Harbours and estuaries, as centres for shipping and aquaculture, have received far larger inputs of exotic marine organisms than have open coast and ocean areas.

Second, human-associated mechanisms that transport organisms around the world, either intentionally or accidentally, primarily take those organisms from areas of substantial human activity. Thus we mainly move organisms that are adapted to, or are tolerant of, substantial human-caused disturbance (Williamson 1996; Cohen & Carlton 1998). Crop and livestock species and their associates are moved from areas of agriculturally related disturbance; people and goods travelling long distances generally begin their journeys in areas subjected to urban disturbance; and ships load goods and ballast water (containing aquatic organisms) from harbour areas, which are often highly altered and heavily polluted environments.

Third, areas disturbed by human activity, such as agricultural lands and lands associated with human habitation, are of substantial importance to humanity and are generally nearer to research institutes than are pristine areas. If, either because of importance or proximity, human-disturbed habitats are more intensively studied than pristine ones, then exotic species are more likely to be detected in them (Simberloff 1986, 1989).

The problem of acceptably sorting environments into more disturbed and less disturbed categories, combined with the difficulty of finding adequate data on successful and unsuccessful inoculations of exotic species into these environments, has made analysis of this question particularly challenging. In the only pertinent study I could find, Hall and Ehler (1979) analysed data from Clausen (1978) on arthropods used to control insects and arachnids, sorting the data into releases in three habitat types: (i) the most unstable or frequently disturbed sites, consisting of annual or short-cycle crops including most vegetable and field crops; (ii) sites with an intermediate level of disturbance, including orchards and other perennial crop systems; and (iii) sites with the least disturbance, including forest and rangeland. They found that the rate of establishment increased as the level of disturbance decreased, with a highly significant increase between the greatest and least levels of disturbance, contrary to conventional wisdom (Table 18.7). Analysing Canadian data in a similar manner, they found that the released organisms established most successfully at intermediate levels of disturbance, and least successfully at the greatest levels of disturbance (Table 18.7). As noted above, there may be problems with using results derived from biocontrol releases to draw conclusions about natural communities. At a minimum, however, there appears to be no published statistical support for the idea that habitats that have been disturbed are more easily invaded.

Table 18.7 Establishment of biocontrol agents at different levels of disturbance. (Adapted from Hall & Ehler 1979.)

<i>Based on worldwide data from Clausen (1978)</i>		
Habitat type:	<i>n</i>	Rate of establishment
Greatest level of disturbance	640	0.28
Intermediate level of disturbance	916	0.32
Least level of disturbance	535	0.36
Habitats compared:	χ^2	<i>P</i>
Greatest vs. intermediate disturbance	3.19	>0.05
Intermediate vs. least disturbance	2.72	>0.05
Greatest vs. least disturbance	9.66	<0.005
<i>Based on Canadian data from Beirne (1975)</i>		
Habitat type:		Rate of establishment
Greatest level of disturbance (annual crops)		0.16
Intermediate level of disturbance (orchards and ornamental shrubs)		0.43
Least level of disturbance (forests)		0.23

Are prolific organisms more successful as invaders?

It has often been proposed that successful invaders are characterized by a large reproductive potential or intrinsic rate of increase (e.g. MacArthur & Wilson 1967; Crawley 1986, 1987; Pimm 1989). Crawley (1986) described the components of the intrinsic rate of increase as fecundity, survivorship and developmental rate, and annual fecundity is a function of both clutch size and the number of clutches per year. Several studies have analysed some of these factors relative to the rate of successful establishment, with variable but usually non-significant results (Table 18.8). Some limitations of these studies should be noted. Analyses based on colonizations effected across natural dispersal distances (O'Connor 1986) may not apply to longer-distance, human-mediated inoculations. Analyses based on translocated species (Newsome & Noble 1986; Griffith *et al.* 1989), which include both species released within their historic ranges and species released outside those ranges, may not apply to introductions of exotic species, which by definition are invasions outside their native ranges. Analyses based on biocontrol agents (Crawley 1986, 1987), which are typically released into habitats with diminished native biota and with the targeted pest providing abundant food resources for the released agent, may have limited relevance to invasions in natural communities. Green's (1997) different analyses of exotic birds in New Zealand yielded both positive and negative relationships (before Bonferroni correction) of clutch size with success, but these became non-significant when analysed for within-family variation, suggesting caution when interpreting analyses that have not accounted for between-family variation. Overall these analyses provide little or no support for hypotheses that organisms exhibiting one or another component of a high reproductive potential are more likely to become established when released into a new environment. On the other hand, Crawley's (1996, 1997) analyses of data on biocontrol insects suggest the possibility

Table 18.8 Relationship of fecundity variables to success in the establishment of species. The effect of an increase in the variable (greater, faster) is reported as significantly increased success (+), significantly decreased success (–) or no significant difference (ns). O'Connor (1986) provided data but no statistical analysis on the greater success of multibrooded bird species as colonists; the effect, as reported here, is not significant ($n=48$, $df=1$, $\chi^2=2.82$, $P>0.05$). Griffith *et al.* (1989) reported a significantly higher success rate in translocated animals with large clutches and early breeding based on a value of $0.05 \leq P \leq 0.1$, but this is reported more conventionally here as not significant.

Variable analysed	<i>n</i>	Effect	Reference
Seasonal egg production in birds colonizing Britain	48	+	O'Connor 1986
Broods per season in birds colonizing Britain	48	ns	After O'Connor 1986
Clutch size of foreign bird species released in Australia	61	ns	Newsome & Noble 1986
Clutch size of translocated bird species released in Australia	47	ns	Newsome & Noble 1986
Fecundity of biocontrol insects:			
on <i>Opuntia</i>	≤22	ns	Crawley 1986
on <i>Lantana</i>	≤30	ns	
on other weeds	≤173	+	
Developmental rate of biocontrol insects:			
on <i>Opuntia</i>	≤22	ns	Crawley 1986
on <i>Lantana</i>	≤30	+	
on other weeds	≤173	ns	
Intrinsic rate of increase (indirectly calculated) of biocontrol insects:			
on <i>Opuntia</i>	≤22	+	Crawley 1987
on <i>Lantana</i>	≤30	+	
on other weeds	≤173	+	
Clutch size and early/late breeding in translocated mammals and birds in Australia, Canada, Hawaii, New Zealand and the USA	198	ns	Griffith <i>et al.</i> 1989
Clutch size of exotic bird species released in New Zealand	79	ns	Veltman <i>et al.</i> 1996
Broods per season in exotic bird species released in New Zealand	79	ns	Veltman <i>et al.</i> 1996
Maximum reported egg production of exotic fish species released into the San Francisco Bay watershed	42	ns	Cohen 1996
Mean clutch size of exotic bird species released in New Zealand:			
variable treated on its own	47	–/ns	Green 1997
in selected regression model	47	–/ns	(with / without
in selected regression model, analysis of within-family variation	36	ns/ns	Bonferroni adjustment)
in selected regression model including only British birds	27	+/ns	

that studies addressing the intrinsic rate of increase, rather than components of the rate of increase, may yet reveal a consistent relationship.

Do invading organisms benefit by leaving their parasites behind?

It has been proposed that invading species gain an advantage by losing parasites when they are transported from their native region, so that in the invaded region

Table 18.9 Parasitization rates in native and exotic fish in northern California. (Based on data from Haderlie 1953.)

	Native fish		Exotic fish		χ^2	P
	n	Fraction parasitized	n	Fraction parasitized		
Centrarchidae	18	0.44	485	0.70	7.7	<0.0055
Cyprinidae	415	0.66	71	0.68	0.1	<0.7644
Salmonidae	141	0.56	38	0.87	12.1	<0.0005
All fish	960	0.63	1038	0.77	45.0	<0.0001

they host fewer parasite species and smaller numbers of parasites than do their potential competitors (Dobson & May 1986). Parasites may be lost through the chance absence of a parasite species from the founding population, through the mortality of infected hosts during transport, and through the absence of suitable intermediate hosts in the invaded region (Dobson & May 1986; Guégan & Kennedy 1993). This 'lost parasites' hypothesis has provided one of the main rationales for classic biological control, which has frequently sought to identify and import the parasites lost by invading species (Simmonds *et al.* 1976; Van den Bosch *et al.* 1982).

One prediction of the lost parasites hypothesis is that successful invading species will host fewer species of parasites and have a smaller parasite burden than do competing native species. To test this, I analysed data from three studies of fish parasites in California that examined both native and exotic fish, comparing both parasite species richness and the host parasitization rate (the fraction of fish in the population that carry some parasites) (Cohen 1996). In these studies, overall and within families that included both native and exotic fish, parasitization rates were usually higher for exotic species, sometimes very significantly so, contrary to the hypothesis (Table 18.9). The mean number of parasite species per fish species was also more often higher for exotic than for native fish.

One possible explanation is that California is a special case. Most fish introduced into the state came from regions with richer fish faunas. These regions may also have richer fish parasite faunas, so that even after losing some parasites, invading fish could still host more parasites than do native fish. If true, however, and if in general having fewer parasites confers a competitive advantage, then California's native fish communities should have been especially resistant to invasion. Instead they have been extensively invaded (Moyle 1976).

Another possibility is that the invading fish may have benefited by retaining their parasites. These may have prevented native California fish parasites from attacking the invading fish (by competitive exclusion); or parasites that arrived with the invading fish may have attacked competing native fish. Since parasite strains or species that are new to a host are often more harmful than parasites to which the host has a history of exposure (Esch & Fernández 1993), retaining its natural parasites could provide substantial benefits to an invading host both by reducing its vulnerability to

novel parasites and by increasing its competitors' exposure to novel parasites. The value to invaders of carrying parasites or diseases with them has been documented most extensively for human invasions—historical studies have shown that smallpox and other diseases carried by European soldiers and settlers, rather than superior military technology, led to the rapid destruction and successful invasion of aboriginal human populations in many regions of the globe (e.g. Crosby 1986).

Conclusions

It has been often stated in the scientific literature that testing for the characteristics that either enable invading organisms to become established or that make environments more vulnerable to invasion, requires data on the rates of success and failure in becoming established. Surprisingly, given the level of interest and the volume of published material on this subject, few such analyses have been done. Data on intentional releases of biocontrol agents, birds, fish, and possibly mammals and shellfish, must surely exist for many regions, though compiling the data in an appropriate form for analysis is time consuming. There are often significant problems with such data—including uncertainties due to the vagaries of reporting and possible confounding factors in the manner and size of the releases—but as it is the best data we have, we should make more thorough use of it.

From the data and analyses reviewed for this chapter, there appears to be little evidence that disturbed habitats are especially vulnerable to the establishment of exotic species and some evidence to the contrary; no clear evidence that prolific organisms are more successful at establishing than less prolific ones; and some counterevidence to the hypothesis that species improve their ability to establish by shedding their native parasites. There does, however, appear to be some good quantitative evidence that islands are more vulnerable than continents are to invasions. The studies reviewed here all involved data on animal invasions, as, surprisingly, there appear to be no published statistical analyses of the success in establishment of introduced plants relative to these four characteristics. Most analyses of the success of plant invasions focus instead on the postestablishment spread of plants. Further analyses of data on establishment rates could only improve the current situation, wherein many researchers and resource managers believe it has been proven that certain characteristics of organisms or environments increase the probability of exotic species becoming established, when in fact these propositions have only rarely been tested, and when tested have mainly produced ambiguous or contradictory results.

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