

BioScience, 2001, Volume 51, Issue 9, Pages 780-789

ISSN: (Print 0006-3568) (Online 1525-3244)

doi: 10.1641/0006-3568(2001)051[0780:BITDSC]2.0.CO;2

<http://www.aibs.org/bioscience/>

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Biological Invasion Theory: Darwin's Contributions from *The Origin of Species*

STUART A. LUDSIN AND ANDREA D. WOLFE

Exotic (nonindigenous) species introductions represent a major threat to both society and the world's biota. From an economic standpoint, the costs associated with species introductions have been high. During 1906–1991, monetary damages resulting from the establishment of 79 exotic species in the United States approximated \$97 billion (OTA 1993). Now, however, with the introduction of about 50,000 nonnative species into the United States, economic damages (which also include control costs) are approximated at \$137 billion per year (Pimentel et al. 2000). Beyond these economic considerations, many of the world's ecosystems have suffered severe ecological damage—upon which no monetary value can be placed—following the introduction of exotic species. This damage, resulting from a variety of mechanisms (e.g., competition, predation, hybridization), has included restructuring of populations and communities, alteration of large-scale ecosystem processes, and loss of biodiversity (Lodge 1993a, 1993b, Williamson 1996, Vitousek et al. 1997, Pimentel et al. 2000). Owing to the negative impacts successful invaders can have on ecosystems, one can easily understand why human-based exotic species invasion is considered a leading threat to biodiversity (Vitousek et al. 1997, Sala et al. 2000) and most likely has contributed significantly to the recent increase in earth's extinction rate, which is equal in magnitude to prehuman periods of mass extinction (Lawton and May 1995, Pimm et al. 1995).

Because of the increase in biological invasions during the 20th century (Mills et al. 1993, Lodge 1993a, Williamson 1996), research aimed at describing, understanding, and predicting species invasions has increased. In fact, interest in the process of biological invasions has been so overwhelming recently that its study has developed into a new subfield within ecology (Lodge 1993a), with its own theory and conceptual framework (e.g., Moyle and Light 1996, Williamson 1996). But just how novel is this subfield, given that much of what we know today about biological invasions—and accept as conventional wisdom—is similar to ideas espoused by 19th-century ecologists? In this article, we attempt to answer this question by focusing on ideas presented by Charles

Darwin in *The Origin of Species*. Toward this end, we demonstrate that Darwin knew about and appreciated biological invasions, and that the current conceptual framework underlying biological invasions is akin to insights within Darwin's seminal text. Ultimately, in discussing these parallels, we seek to bestow more kudos upon the already honored Charles Darwin.

Sources of information: Darwin and modern-day ecologists

This essay is neither a comprehensive review of biological invasion theory nor a critical evaluation of the ideas (or paradigms) espoused by modern-day ecologists or Darwin. Such an undertaking would have been monumental, detracting from our central purpose. Thus, we include only enough of the primary literature to demonstrate that Darwin's views on biological invasions, as taken from the second edition of *On the Origin of Species By Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (1859; cited text, however, corresponds with Darwin 1996), parallel the thoughts and ideas espoused by contemporary ecolo-

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gists and evolutionary biologists (regardless of whether they are correct). Although many excellent, comprehensive texts and papers have been published on biological invasions (see Lodge 1993b, Williamson 1996), most of the contemporary views presented herein derive from Williamson (1996). We selected Williamson's (1996) set of ideas for two reasons. First, no other document has synthesized all phases of biological invasion (arrival and establishment, spread, equilibrium and effects, and implications) into a concise, organized, and cohesive framework (but see Moyle and Light 1996). Second, although Williamson (1996) did not find any unconditional rules that govern invasions, he nicely characterized the current conventional wisdom and its weaknesses.

The Origin of Species is not a text exclusively about biological invasions. As such, ideas related to biological invasions were not presented in a cohesive, straightforward manner. Within this text, however, we found dozens of statements about characteristics of species and communities that influence invasion success, as well as information relating to why we need to be concerned about species introductions (i.e., a conceptual framework). Below, we contrast Darwin's invasion model, as constructed from statements in *The Origin of Species*, with the first 10 points of Williamson's (1996) conceptual framework (Table 1).

A comparison of conceptual frameworks

Following the organization of Williamson (1996), we grouped conceptual framework points in order to delineate among the various stages of the biological invasion process. We first discuss factors concerning the arrival and establishment of a species in a new environment ("Arrival and Establishment"). We then proceed (chronologically) to discuss factors relating to its spread in that environment ("Spread"), as well as the potential effects an invader can have on the invaded ecosystem once it has become established ("Equilibrium and Effects"). We conclude our comparison of Darwin's and Williamson's ideas by discussing how an exploration of biological invasions can aid our understanding of ecological and evolutionary processes ("Implications").

Arrival and establishment

Conceptual framework point (CFP) 1: Most arrivals at present are from human importations, but natural arrivals also are of interest. Although most recent investigations of biological invasions have focused on those stemming from anthropogenic influences (Mills et al. 1993, Vitousek et al. 1997), Williamson (1996) reminds us that species introductions also occur naturally. Lodge (1993a, p. 133) also holds this view, having proposed "biological invasions are commonplace in nature, and should not, in general, be viewed as abnormal events" (also see Elton 1958, Ashton and Mitchell 1989, Carlton 1996). As further support, Williamson and Brown (1986) demonstrated that more than 75% of exotic avian species entering Britain did so without human involvement. Similarly, a recent hurricane in the Caribbean, which transported green iguanas (*Iguana iguana*) from Guadeloupe to Anguilla, has

reincited the debate about the importance of natural dispersal as a mechanism for understanding the biogeography of terrestrial animals (Censky et al. 1998).

As with contemporary scientists, Darwin grasped the regularity and potential significance of natural invasions. In fact, he used it to help account for the nonintuitive biogeographical distribution of species, while also lending support for his theory of evolutionary change. Darwin (1996) went to great lengths to describe how species invasions deriving from glaciation events, operating on evolutionary time scales (pp. 295–309), and "accidental means" (p. 290), operating on ecological time scales (e.g., plants, seeds, mussel or clam veligers transported on the foot of a duck, pp. 290–293, 311–314; seeds carried in the digestive tract of fish and birds, pp. 292–293, 313; birds blown across the sea, pp. 292, 313; seeds drifting in oceanic currents, pp. 290–291), could help explain discrepancies among biogeographical patterns, as evidenced from the fossil record (Table 1).

Of greater importance, at least on an ecological time scale, are human-assisted introductions, which have increased the rate of biological invasions to the fastest in Earth's history (Lodge 1993a, 1993b, Williamson 1996, Vitousek et al. 1997). Carlton and Geller (1993) speculate that on any single day, more than 3000 species may be contained within the ballast water of oceangoing ships, potentially leading to the introduction of tens of thousands of species into foreign areas annually (Carlton 1996). Likewise, Mills et al. (1993) showed that, although exotic species introductions have occurred in the Great Lakes since the early 1800s, the rate of introduction has increased since that time, with nearly one-third of invasions occurring during the last 30 years.

Although humankind's role in species introductions is emphasized more in recent literature than in *The Origin of Species*, Darwin did recognize that role. He wrote, for example, that "the rat and mouse...have been transported by man to many parts of the world, and now have a far wider range than any other rodent" (Darwin 1996, p. 116). Similarly, Darwin (1996, p. 318) credited humankind for the presence of terrestrial mammals on oceanic islands: "As yet I have not found a single instance, free from doubt, of a terrestrial mammal (*excluding domesticated animals kept by natives* [emphasis added]) inhabiting an island situated above 300 miles from a continent or great continental island." Other examples regarding the human-assisted spread of exotic species ("domestic productions") also can be found in *The Origin of Species* (Table 1).

CFP 2: Most invasions fail; only a limited number of taxa succeed (the "tens rule"). Contemporary theory suggests that invasion success is low, with the probability of success following a statistical rule, namely, the "tens rule" (Williamson and Brown 1986, Williamson 1996). A broad generalization spanning a wide range of taxa (including both plants and animals), the tens rule states that only 10% of introduced (or feral) species will become established (i.e., form self-sustaining populations, become naturalized), and of that 10%, only 10% will grow enough in number to become nuisance or pest species (i.e., have a negative economic effect).

Table 1. Comparison of an invasion model constructed from statements taken from the second edition of Darwin's *On the Origin of Species By Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life (1859)*, and present-day conceptual framework advanced by Williamson (1996).

Conceptual framework points (CFPs) from Williamson (1996)	Support from Darwin's <i>The Origin of Species</i> ^a	Support from the primary literature
1. Most arrivals at present are from human importations, but natural arrivals also are of interest.	pp. 91, 94–95, 116, 258, 290–314, 318–319, 325	Ashton and Mitchell (1989), Carlton and Geller (1993), Lodge (1993a, 1993b), Mills et al. (1993), Carlton (1996), Williamson (1996), Vitousek et al. (1997)
2. Most invasions fail; only a limited number of taxa succeed ("tens" rule).	pp. 58, 65	Williamson and Brown (1986), Ehrlich (1989), Williamson (1992), Lodge (1993a, 1993b), Moyle and Light (1996), Williamson (1996), Vitousek et al. (1997)
3. Invasion (or propagule) pressure is an important variable, so invasions are often to accessible habitats by transportable species.	pp. 290–295, 307, 310–314, 316–321, 327–328	Bazzaz (1986), Simberloff (1989), Mills et al. (1993), Carlton (1996), Moyle and Light (1996), Williamson (1996)
4. All communities are invasible, perhaps some more than others.	pp. 69, 91, 164, 319, 381	Elton (1958), Moyle et al. (1986), Orians (1986), Pimm and Hyman (1987), Usher (1988), Carlton (1996), Moyle and Light (1996), Williamson (1996), Vitousek et al. (1997), Lonsdale (1999), Stohlgren et al. (1999)
5. The a priori obvious is often irrelevant to invasion success. Among factors to consider: the intrinsic rate of natural increase (<i>r</i>), abundance in native habitat, taxonomic isolation, climatic and habitat matching, vacant niches.	pp. 55, 65, 88, 94–95, 98, 263, 283, 307, 314, 325	Elton (1958), Simberloff (1981), Moyle (1986), Orians (1986), Moulton and Pimm (1986), Pimm and Hyman (1987), Ashton and Mitchell (1989), Ehrlich (1989), Pimm (1989), Simberloff (1989), Lodge (1993a), Moyle and Light (1996), Williamson (1996), Lonsdale (1999), Stohlgren et al. (1999)
6. Spread can be at any speed in any direction.	pp. 54–55, 88, 263–264, 306–307, 310–315, 324–325	Williamson (1996), McKinney and Lockwood (1999)
7. Most invaders produce minor consequences (tens rule).	pp. 58, 65, 91	See references for CFP 2
8. The consequences of invasions can be severe, ranging from depressed populations to individual extinctions to ecosystem restructuring, and the causal mechanisms driving these changes can be diverse.	pp. 55, 59–60, 68, 164, 258, 304, 307, 315	Zaret and Paine (1973), Vitousek and Walker (1989), Spencer et al. (1991), Witte et al. (1992), Moyle and Light (1996), Rhymer and Simberloff (1996), Williamson (1996), Vitousek et al. (1997), Fritts and Rodda (1998), Schulz and Yurista (1998), Ayres et al. (1999), McKinney and Lockwood (1999), Parker et al. (1999)
9. Genetic factors may determine invasion success; genetic factors affect events at the initial invasion; evolution may occur after invasion.	pp. 50, 94–95, 98	Martins and Jain (1979), Philipp (1991), Ryman et al. (1995), Rhymer and Simberloff (1996), Williamson (1996), Ayres et al. (1999), Parker et al. (1999)
10. Invasions are informative about the structure of communities and the strength of interactions, and	pp. 95, 283, 307	Moyle et al. (1986), Simberloff (1989), vice versa. Lodge (1993a, 1993b), Williamson (1996)

^a Page numbers correspond to those in Darwin (1996).

Williamson (1992) has demonstrated that the rule has some roughness, in that values tend to range from 5% to 20%. Lodge (1993b) settled upon a higher maximum value (i.e., 38%) for successful invasions, but suggested that this value may be biased high because many studies failed to document unsuccessful invaders, focused only upon easily observed species, or had a narrow taxonomic basis. Although deviations from the rule exist (Lodge 1993a, Williamson 1996), as a predictor of invasion success, the tens rule has held true for a variety of organisms, including angiosperms, grasses, legumes, terrestrial vertebrates, fishes, mollusks, and plant pathogens (Lodge 1993a, 1993b; Mills et al. 1993; Williamson 1996, Fig. 2-2).

Darwin did not attempt to derive a statistical rule to describe the probability of invasion success. However, he did recognize that not all nonindigenous species would successfully colonize their new environment. Theorizing that native species are more suitably adapted to their environments than invaders, Darwin (1996, p. 65) wrote, "we can see that when a plant or animal is placed in a new country amongst new competitors, though the climate may be exactly the same as in its former home,...the conditions of its life will generally be changed in an essential manner."

Darwin (1996, p. 65) also suggested that the only means for an exotic species to establish itself successfully ("increase its average numbers in its new home") would be to "modify it in a different way to what we should have done in its native country; for we should have to give it some advantage over a different set of competitors or enemies." Thus, although we cannot be certain that Darwin would have supported all facets of the tens rule, we are confident that he would have accepted its main precept: Not all exotic species introductions will succeed.

CFP 3: Invasion (or propagule) pressure is an important variable, so invasions are often to accessible habitats by transportable species. Because the probabilities of finding a mate (for those invaders that rely on sexual reproduction) and escaping elimination by pressures associated with weather, predators, and parasites increase with propagule pressure (i.e., the number of individuals that invade habitat; Williamson 1996), species that can easily cross geographical barriers; have resistant, highly dispersive seed or larval stages; or are highly fecund are expected to be successful invaders. Indeed, much empirical evidence supports this contention, which helps to explain the high invasion success of bird (Williamson 1996), fish (Mills et al. 1993), insect (Simberloff 1989), and plant (Bazzaz 1986) species.

Darwin (1996, p. 310) also recognized the importance of dispersal, resistance to desiccation, and fecundity to the successful establishment of exotics (Table 1): "This power in fresh-water productions of ranging widely...I think, in most cases can be explained by their having become fitted, in a manner highly useful to them, for short and frequent migrations." Darwin (1996, p. 314) later wrote that "the wide distribution of fresh-water plants and of the lower animals...I believe mainly depends on the wide dispersal of their seeds and eggs." Examples of organisms likely to be successful in-

vaders that were mentioned by Darwin (1996) include aquatic plants (e.g., *Helosciadium*, *Nelumbium luteum*, *Potamogeton*; pp. 290, 313) and invertebrate animals (e.g., the mollusk *Ancylus*, a *Colymbetes* "water-beetle," p. 312), as well as terrestrial animals that have evolved the ability to fly (e.g., birds, bats; pp. 292, 319) (Table 1). In fact, Darwin (1996) suggested that the scarcity of terrestrial mammals (excepting bats, because of their ability to fly; p. 319) and amphibians (i.e., "frogs, toads, and newts"; p. 318) on "so many oceanic islands cannot be accounted for by their physical conditions" but by their "great difficulty in their transportal across the sea" (p. 318). Through the use of empirical observation and experimentation, Darwin attributed the invasion success of these species to adaptations that allow them either to survive harsh conditions (e.g., prolonged exposure to salt water, air, or digestive juices within the stomachs of fish and birds; pp. 290–293, 312–313) or to be transported by natural processes (e.g., wind and water currents) across great distances and for long periods of time (pp. 290–293, 312–313). That Darwin's stereotypical successful invader was more *r*-selected (i.e., highly fecund, high rate of per-capita population growth (*r*), tolerance for a wide range of conditions, capability of rapid dispersal) than *K*-selected (i.e., low fecundity, low *r*, poor dispersal and colonizing abilities) meshes well with the current conventional wisdom (Lodge 1993a, 1993b, Williamson 1996).

CFP 4: All communities are invisable, perhaps some more than others. One generalization that has become crystallized in our reading of the invasion literature is that all habitats can be invaded, including protected nature preserves and national parks (Elton 1958, Moyle et al. 1986, Moyle and Light 1996, Williamson 1996, Lonsdale 1999, Stohlgren et al. 1999). In a review of plant invasions in US national parks and preserves, Vitousek et al. (1997) demonstrated that exotic vascular plants comprise 5% to 25% of the flora in many of these protected areas, whereas nonnatives contribute 50% to 70% of the flora in Hawaiian reserves. Likewise, in a study of 23 nature preserves worldwide, Usher (1988) documented that each contained at least one exotic vertebrate and several invasive vascular plant species. In fact, 18% of terrestrial vertebrates and 30% of the vascular plant species across Usher's study preserves were nonindigenous. Interestingly, Usher (1988) and Lonsdale (1999) both demonstrated that the susceptibility of these "protected" environments to plant invasion was positively related to the number of visitors to the park (i.e., humans serve as a mechanism to increase transport of seeds or fragments, and ultimately propagule pressure).

Even though all communities (and ecosystems) appear susceptible to invasion, Williamson (1996) suggests that disturbed habitats are more prone to successful establishment of exotics than are pristine ones. In the first text specifically dedicated to biological invasions, *The Ecology of Invasions by Animals and Plants*, Elton (1958) also suggested that anthropogenic disturbance increases the likelihood of exotic establishment. Elton specifically identified simplified habitats (e.g., monocultures produced by humans) as being highly vulnerable to exotic invaders, and that human population growth

and expansion into new territories, “resulting in unnatural disturbance,” have led to an increase in biological invasions of late. Although theoretical and empirical investigations support the notion that disturbed areas are more likely to be invaded than nondisturbed ones (e.g., Orians 1986, Pimm and Hyman 1987, Carlton 1996, Moyle and Light 1996), the true role disturbance plays in biological invasion success remains unresolved (Ashton and Mitchell 1989, Simberloff 1989, Lodge 1993a, 1993b, Williamson 1996, Stohlgren et al. 1999).

Like contemporary ecologists, Darwin recognized that no system is impervious to invasion (Table 1). Using outcomes of human colonization attempts to support this contention, Darwin (1996, p. 69) wrote that

No country can be named in which all the native inhabitants are now so perfectly adapted to each other and to the physical conditions under which they live, that none of them could anyhow be improved; for in all the countries, the native have been so far conquered by the naturalised productions, that they have allowed foreigners to take firm possession of the land. And as foreigners have thus everywhere beaten some of the natives, we may safely conclude that the natives might have been modified with advantage[s], so as to have better resisted such intruders.

In later references that now concern plants and animals, Darwin (1996) wrote, “The endemic productions of New Zealand, for instance, are perfect one compared to another; but they are now rapidly yielding before the advancing legions of plants and animals introduced from Europe. Natural selection will not produce absolute perfection, nor do we always meet, as far as we can judge, with this high standard under nature” (p. 164). “Hardly an island can be named on which our smaller quadrupeds have not become naturalised and greatly multiplied” (p. 319).

Clearly, these statements support our hypothesis that Darwin recognized that all communities—even those with perfectly coevolved species complexes—are still vulnerable to invasion by nonindigenous plants and animals.

CFP 5: The a priori obvious is often irrelevant to invasion success. Among factors to consider: the intrinsic rate of natural increase (r), abundance in native habitat, taxonomic isolation, climatic and habitat matching, vacant niches. The final aspect of the “arrival and establishment” phase of Williamson’s (1996) conceptual framework concerns our ability to predict invasion success. In general, Williamson (1996, p. 77) suggests that our predictive ability is limited, and that “an invader can be any sort of species going into any sort of habitat.” His evaluation of both species (e.g., r , genetic structure, modes of reproduction) and community (e.g., species richness, climate, vacant niches) characteristics indicates that generalities encompassing wide taxonomic ranges are not possible, given the large number of exceptions. In fact, Williamson (1996) suggests that only propagule pressure and previous invasion success in other habitats are consistent predictors of invasion success (but see Ehrlich 1989).

Even though disagreement exists among ecologists regarding predictors of biological invasion success (Ashton and Mitchell 1989, Ehrlich 1989, Simberloff 1989, Williamson

1996, Stohlgren et al. 1999), a close match exists between Darwin and contemporary ecologists regarding species and community attributes that promote successful introductions. For example, relative to species characteristics, Darwin recognized that species with previous invasion success will likely be successful invaders in the future; “It is also natural that the dominant, varying, and far-spreading species, which already have invaded to a certain extent the territories of other species, should be those which would have the best chance of spreading still further” (Darwin 1996, p. 263). The notion that previous invasion success and the geographical range of species may be indicative of future invasion success is supported by the primary literature (e.g., Moulton and Pimm 1986, Williamson 1996). In his discussion of the success of naturalized plants throughout Asia and North America, Darwin (1996, p. 55) argued that “the geometrical ratio of increase...simply explains the extraordinarily rapid increase and wide diffusion of naturalised productions in their new homes.” And, despite being ignorant of Mendelian genetics, Darwin’s (1996, p. 98) ability to recognize that “the more diversified in structure the descendants from any one species can be rendered, the more places they will be enabled to seize on, and the more their modified progeny will be increased” clearly portrays the wisdom of this thinker.

Darwin also recognized that characteristics of an invaded habitat can influence invasion success. As gleaned from his detailed discussions of natural selection, Darwin (1996, p. 65) apparently believed that biotic interactions (i.e., competition and predation) would be major regulators of invasion success:

We can see that when a plant or animal is placed in a new country amongst new competitors, though the climate may be exactly the same as in its former home, yet the conditions of its life will generally be changed in an essential manner. If we wished to increase its average numbers in its new home, we should have to modify it in a different way to what we should have done in its native country; for we should have to give it some advantage over a different set of competitors or enemies.

Owing to the potential importance of competition to biological invasion success, Darwin (1996, pp. 94–95) speculated that successful invaders will be species that can take advantage of open niches and that are diversified in structure (i.e., morphologically or behaviorally different) relative to indigenous species:

The truth of the principle, that the greatest amount of life can be supported by great diversification of structure, is seen under many natural circumstances.... It is seen, that where they come into the closest competition with each other, the advantages of diversification of structure, with the accompanying differences of habit and constitution, determine that the inhabitants, which thus jostle each other most closely, shall, as a general rule, belong to what we call different genera and orders.

The same principle is seen in the naturalisation of plants through man’s agency in foreign lands. It might have been expected that the plants which have succeeded in becoming naturalised in any land would generally have been closely allied to the indigenes... It might also, perhaps have been expected that the naturalised plants would have belonged to a

few groups more especially adapted to certain stations in their new homes. *But the case is very different.... These naturalised plants are of a highly diversified nature. They differ, moreover, to a large extent from the indigenes* [emphasis added].

Further highlighting the potential role of competition and open niches to invasion success, Darwin (1996) hypothesized that the probability for invasion would be greater in small, freshwater systems than in large, continental systems: “As the number of kinds is small, compared with those on the land, the competition will probably be less severe between aquatic than between terrestrial species; consequently an intruder from the waters of a foreign country, would have a better chance of seizing on a place, than in the case of terrestrial colonists” (p. 314).

Although the importance of vacant niches and species diversity to the success of biological invasions remains a contentious issue (Stohlgren et al. 1999), many contemporary ecologists have used reasoning analogous to that of Darwin to explain patterns of invasion success. For example, Moyle (1986) used vacant niche theory to help explain why exotic fishes have been more successful at invading western reservoirs (those with low species diversity) than eastern reservoirs (those with high diversity) in the United States. Likewise, our understanding of the success of many exotic fish species in the Great Lakes appears to be linked to the decimation of ecologically similar native species (Pimm and Hyman 1987, Moyle and Light 1996). Further, contemporary ecologists still use Darwin’s (1996) reasoning that “[on] a small island, the race for life will have been less severe” (p. 88) to explain why small islands of low diversity have been more prone to successful invasion than large, speciose continents (Elton 1958, Orians 1986, Pimm 1989). In fact, Moyle and Light (1996) developed a general empirical rule for freshwater invasions, which suggests that systems with disrupted native assemblages (i.e., those with open niches) are most prone to invasion (also see Simberloff 1981, Lodge 1993a).

We conclude the discussion of CFP 5 by noting what scientists, old and new, have to say about our ability to predict invasion success. Darwin (1996, p. 65) stated that “it is good thus to try in our imagination to give any form some advantage over another. Probably in no single instance should we know what to do, so as to succeed. It will convince us of our ignorance on the mutual relations of all organic beings; a conviction as necessary, as it seems difficult to acquire.”

He added (p. 307) that “I am far from supposing that all difficulties are removed...in regard to the range and affinities of the allied species which live in the northern and southern temperate zones.... I do not pretend to indicate the exact lines and means of migration [i.e., invasion], or the reason why certain species and not others have migrated.”

Ironically, almost 140 years later ecologists are drawing the same conclusions as Darwin. Lodge (1993a, p. 135) suggested that “because all patterns are characterized by large variance and exceptions, we cannot with any confidence predict the outcome of any particular introduction. For successful prediction, every potential invader and target community must be intensively studied.” Similarly, Ehrlich (1989, p. 326) stated

that “ecologists can make some powerful and wide-ranging predictions about invasions.... On the other hand, ecologists cannot accurately predict the results of a single invasion or introduction event.” Clearly, our inability to forecast species reflects the complex nature of ecological interactions (Ehrlich 1989).

Spread

CFP 6: Spread can be at any speed in any direction. Although Williamson (1996) appears pessimistic about our ability to predict invasion success, he feels that our capacity to predict rates of spread following establishment may be greater. In general, Williamson (1996) suggests that, although the rate and direction of spread can be of any speed or direction, knowledge of the intrinsic rates of increase and diffusion may aid our predictive capabilities. Admittedly, Darwin’s discussions of rates of spread are limited. Yet, he did acknowledge “the fact that many species, naturalised through man’s agency, have spread with astonishing rapidity over new countries...[and] that most species would thus spread” (p. 325). Darwin (1996) also mentioned attributes that very likely govern the rate of spread and “process of diffusion,” such as the geometrical rate of increase (pp. 54–55, 263), competitive abilities (pp. 87–88, 263), ecological and evolutionary history of the species (pp. 263–264), dispersal mechanisms (pp. 310–315), biotic interactions (i.e., “the conditions of life”; pp. 263, 324), and climatic and geographic features (pp. 263, 306–307) (see Table 1).

Equilibrium and effects

CFP 7: Most invaders produce minor consequences (tens rule). Although exotic invaders can cause extensive ecological, evolutionary, and economic damage, as an axiom of CFP 2 (i.e., the tens rule), Williamson (1996) suggests that most invaders (about 99%) will have little ecological or economic impact. Darwin did not attempt to quantify the number of invasions that would succeed; however, we found evidence to suggest that he realized that successful invasions would not always have major effects on the invaded community: “Probably no region is as yet fully stocked, for at the Cape of Good Hope, where more species of plants are crowded together than in any other quarter of the world, some foreign plants have become naturalised, without causing, as far as we know, the extinction of any natives” (Darwin 1996, p. 91).

In addition, based on Darwin’s discussions of the importance of the “conditions of life” to invasion success, even suitable climate matches between the invader and the invaded habitat do not guarantee invasion success: “That climate acts in main part indirectly by favouring other species, we may clearly see in the prodigious number of plants in our gardens which can perfectly well endure our climate, but which never become naturalised, for they cannot compete with our native plants nor resist destruction by our native animals” (1996, p. 58). Thus, for an exotic invader to succeed, some major “advantage” over its competitors and predators would be required (Darwin 1996, p. 65).

CFP 8: The consequences of invasions can be severe, ranging from depressed populations to individual extinctions to ecosystem restructuring, and the causal mechanisms driving these changes can be diverse. Conceptual framework point 2 suggests that most invasions have little impact on the biotic and abiotic components of the invaded ecosystem. However, of those systems that are affected, the consequences can be severe, including alteration of population demographics (Moyle and Light 1996, Ayres et al. 1999, McKinney and Lockwood 1999, Parker et al. 1999), community organization (e.g., species composition and abundance, food-web structure; Zaret and Paine 1973, Schulz and Yurista 1998, Parker et al. 1999), and ecosystem function (Lodge 1993b, McKinney and Lockwood 1999, Parker et al. 1999), as well as species extirpation or extinction (Witte et al. 1992, Fritts and Rodda 1998, Ayres et al. 1999).

For example, in Lake Victoria approximately 200 of 300 *Haplochromis* cichlid species—of which 99% were endemic—were driven to extinction primarily by the introduction of piscivorous Nile perch (*Lates niloticus*) during the early 1950s (Witte et al. 1992). In the Flathead catchment, Montana, following the intentional introduction of opossum shrimp (*Myxis relicta*) into Flathead Lake in 1949 to improve the non-indigenous kokanee salmon (*Oncorhynchus nerka*) fishery, kokanee salmon declined in abundance because their preferred prey (cladoceran zooplankton) was, ironically, decimated by *M. relicta* (via both predation and competition) (Spencer et al. 1991). The reduction in kokanee salmon then triggered reductions in eagle, bear, gull, and duck visitations to the lake, ultimately resulting in reduced tourism to the area (Spencer et al. 1991). In Hawaii's Volcanoes National Park, invasion of *Myrica faya*, a nitrogen-fixing tree, altered nutrient cycling in that ecosystem, ultimately changing the "rules of existence" for many species (Vitousek et al. 1997). Specifically, Vitousek and Walker (1989) found that *M. faya* increased the availability of inorganic nitrogen, which is typically a limiting nutrient in this ecosystem, by more than fourfold. This, in turn, allowed other exotic species adapted to high nutrient conditions to dominate these habitats.

A diverse array of mechanisms drives these changes, including vertical food chain effects (i.e., predation; Zaret and Paine 1973, Fritts and Rodda 1998, Schulz and Yurista 1998), horizontal food chain effects (i.e., competition, both interference and exploitative; Moyle and Light 1996, Lodge 1993a), and hybridization (Philipp 1991, Rhymer and Simberloff 1996, Ryman et al. 1995, Ayres et al. 1999, Parker et al. 1999). Because these are only a few of numerous examples of negative impacts of biological invasions, we concur with Vitousek and colleagues (1997) that biological invasions are a "significant component of environmental change."

By contrasting a part of a heath that "had never been touched by the hand of man" (p. 59) with another part that "had been enclosed twenty-five years previously and planted with [exotic] Scotch fir" (p. 60), Darwin (1996) clearly demonstrates his awareness of how "potent" species introductions can be. Specifically, he observed that "the change in the native veg-

etation of the planted part of the heath was most remarkable.... Not only the proportional numbers of the heath-plants were wholly changed, but twelve species of plants (not counting grasses and carices) flourished in the plantations, which could not be found on the [unplanted] heath. The effect on the insects must have been still greater, for six insectivorous birds were very common in the plantations, which were not to be seen on the [unplanted] heath" (p. 60).

In another example, Darwin (1996) relates how important grazing cattle (an introduced herbivore) can be in structuring communities. In areas protected from grazing by enclosures, "it became thickly clothed with vigorously growing young firs. Yet the [unprotected] heath was so extremely barren and so extensive that no one would ever have imagined that cattle would have so closely and effectually searched it for food" (p. 60). Further espousing the potential importance biological invasions can have on communities, Darwin (1996, p. 307) wrote, "In many islands the native productions are nearly equalled or even outnumbered by the naturalised; and if the natives have not been actually exterminated, their numbers have been greatly reduced, and this is the first stage towards extinction." Further, Darwin (1996, p. 315) stated that "there is reason to believe that the naturalised plants and animals have nearly or quite exterminated many native productions." From these examples and others (Table 1), we clearly can see that Darwin recognized that biological invasions can have dramatic effects on invaded communities.

CFP 9: Genetic factors may determine invasion success; genetic factors affect events at the initial invasion; evolution may occur after invasion. Although the recent invasion literature has focused primarily on the importance of abiotic and biotic interactions in governing invasion success, a small, but growing, component has focused on the role of the genetic structure of invaders (e.g., Philipp 1991, Ryman et al. 1995, Rhymer and Simberloff 1996, Ayres et al. 1999, Parker et al. 1999). These investigations have been largely theoretical, exploring the potential significance of a variety of genetic attributes (e.g., ploidy, heterozygosity, asexual versus sexual reproduction) to the success of an invader.

Although a few empirical studies have suggested that heterozygosity is important to the invasion success of plants (e.g., Martins and Jain 1979), the role of genetics is still largely unknown. Williamson (1996), however, suggests that genetic factors most likely are important, given that a slight alteration in a species genome can influence its fitness. In support of this notion, Ayres et al. (1999) demonstrated that an exotic congener caused the local extinction of *Spartina foliosa* (a native cordgrass) via hybridization. Similarly, Philipp (1991) demonstrated that introduced Florida largemouth bass (*Micropterus salmoides floridanus*) readily hybridizes with its northern subspecies (*M. salmoides salmoides*), which, in turn, can negatively affect growth and overwinter survival of the northern subspecies. Ryman and colleagues (1995) also provide numerous examples of how hybridization of cultured fish with wild fish can lead to the loss of coadapted gene complexes and genetic integrity. As such, we concur with Ryman and col-

leagues (1995) that the genetic effects of introduced species is a crucial uncertainty that warrants further study.

Obviously, we cannot argue that Darwin had any thoughts on the importance of the genetic structure of organisms to invasion success because he was not knowledgeable about Mendelian genetics. However, upon examination of his ideas regarding species that succeed in the game of natural selection, we can see that he recognized the potential importance of heritability (albeit in a somewhat Lamarckian sense) and variability to the future success of organisms. "We have, also, seen that it is the most flourishing or dominant species of the larger genera which on an average vary most.... The larger genera thus tend to become larger; and throughout nature the forms of life which are now dominant tend to become still more dominant by leaving many modified and dominant descendants" (Darwin, 1996, p. 50), he wrote.

Later, Darwin (1996, p. 98) stated that "as a general rule, the more diversified in structure the descendants from any one species can be rendered, the more places they will be enabled to seize on, and the more their modified progeny will be increased." Clearly, Darwin was speaking of phenotypic attributes in this instance. His ideas, however, certainly parallel our thoughts on the importance of genetic variability and morphological plasticity to the success of a species. If only Darwin had managed to pick up a copy of Gregor Mendel's *Experiments in Plant Hybridization*....

Implications

CFP 10: Invasions are informative about the structure of communities and the strength of interactions, and vice versa. This CFP focuses on the necessity of understanding the dynamics of biological invasions and communities because of insights they can provide about community organization, processes that regulate invasion success, ecological risks associated with a new invader (including organisms introduced as biological controls), and evolution. Our recent history is checkered by accidental and intentional introductions that caused dramatic ecological and economic damage (e.g., zebra mussels *Dreissena polymorpha*, Nile perch, opossum shrimp, *M. faya*, brown tree snakes *Boiga irregularis*), many of which could have been avoided had we enough foresight to understand the dynamics of the invader and invaded community. We have already mentioned the ecosystem-level effects experienced in the Flathead catchment owing to the intentional introduction of mysids. Similarly, the planned introduction of a predatory snail, *Euglandina rosea*, into Hawaii as a biological control for another nonindigenous snail species (*Achatina fulica*) led to the elimination of all native *Partula* snails, and is expected to eliminate all endemic tree snails (Williamson 1996). For reasons such as these, we can understand why fishery ecologists are warning against the intentional introduction of stocked fishes throughout Europe and North America (Moyle et al. 1986, Philipp 1991, Ryman et al. 1995).

Although the scientific community is only now beginning to recognize that biological invasions can lend insight into eco-

logical and evolutionary processes (e.g., Simberloff 1989, Lodge 1993a, 1993b), Darwin (1996, p. 95) was cognizant of this even before ecology became an organized discipline: "By considering the nature of the plants or animals which have struggled successfully with the indigenes of any country, and have there become naturalised, we may gain some crude idea in what manner some of the natives would have to be modified, in order to gain an advantage over the other natives."

Similarly, he even suggested that knowledge of mechanisms that allow successful colonization of an exotic species may shed insight into the biogeographical distribution and evolutionary success of species: "I do not pretend to indicate the exact lines and means of migration, or the reason why certain species and not others have migrated; why certain species have been modified and have given rise to new groups of forms, and others have remained unaltered. We cannot hope to explain such facts, until we can say why one species and not another becomes naturalised by man's agency in a foreign land" (p. 307).

The Origin of Species: More than a text about natural selection

Certainly, one can argue that Charles Darwin's *The Origin of Species* has been the single most important contribution to modern biology. Almost 140 years since its first publication, Darwin's theory of evolution (with subsequent modifications made by geneticists) is still revered as the most scientifically plausible explanation for speciation, and it has set the foundation for the enormous evolution-based research effort that pervades biology, paleontology, and anthropology. Owing to its impact on how we interpret historical and modern-day biology (e.g., phenotypic and genotypic variation, functional morphology, species diversity, plant and animal behavior), one can easily understand why Futuyma (1995, p. 5) considers evolution to be the "single most pervasive theme in biology, the unifying theme of the entire science."

But *The Origin of Species* is so much more than a seminal text on evolution. Historians and biologists alike have argued that this work provided the basis of modern-day ecology (McIntosh 1985), and a cursory read of *The Origin of Species* will reveal the true roots of many ecological theories and phenomena (e.g., competitive exclusion, limiting similarity, character displacement, predation, sexual selection, kin selection, island biogeography). In fact, Darwin's work has been so influential—mainly those elements relating to evolution—that its impact extends beyond science itself, permeating many aspects of society, including politics, education, and religion (Futuyma 1995, Gould 1999).

Yet, despite all the recognition Darwin's seminal text has received, we still may not have attributed to him all the credit he deserves. For as we have just demonstrated, Darwin spoke authoritatively about the growing subfield of biological invasions. In fact, much of the current conventional wisdom regarding biological invasions was espoused in *The Origin of Species*. Like many contemporary ecologists, Darwin was aware that exploration of the biological invasion process is im-

portant because it can provide insight into how communities are structured, as well as help us understand the biogeographical distribution and evolution of species. Similarly, he recognized that attributes of both the invader and the invaded community can be important to understanding the success of an exotic species in a new environment. Darwin even drew the same conclusions (namely, that our ability to predict the success of invasions will remain limited because of the complexity of ecosystems) that many ecologists now accept as the current conventional wisdom (e.g., Ehrlich 1989, Lodge 1993a).

Given that Darwin's conceptualization of biological invasion success really does not differ much from the present conventional wisdom (regardless of the correctness of ideas, whether old or new), we, like others (Williamson 1996, p. 1, Stohlgren et al. 1999, p. 25), feel that Darwin's insights into biological invasions should be recognized. Quite possibly, had some of Darwin's observations on biological invasions been better noted, we might not be experiencing the severity and variety of problems that we currently face.

Acknowledgments

We thank D. Culver, M. Kershner, M. Greenstone, J. Holomuzki, R. Stein, T. Waite, and two anonymous reviewers for their comments on previous drafts of this manuscript. Support for this work was provided by (1) a Federal Aid in Sport Fish Restoration Project F-69-P (to R. A. Stein), administered jointly by the US Fish and Wildlife Service and Ohio Department of Natural Resources—Division of Wildlife, (2) the Department of Evolution, Ecology and Organismal Biology at The Ohio State University (OSU), and (3) a Presidential Fellowship awarded to S. A. Ludsin by OSU. Final preparation of this manuscript was assisted by support from a Great Lakes Institute for Environmental Research Post-doctoral Fellowship at the University of Windsor awarded to S. A. Ludsin and a Natural Sciences and Engineering Research Council of Canada Strategic Grant (to P. F. Sale and others).

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