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Linking invasions and biogeography: Isolation differentially affects exotic and native plant diversity

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Abstract. The role of native species diversity in providing biotic resistance to invasion remains controversial, with evidence supporting both negative and positive relationships that are often scale dependent. Across larger spatial scales, positive relationships suggest that exotic and native species respond similarly to factors other than diversity. In the case of island habitats, such factors may include island size and isolation from the mainland. However, previous island studies exploring this issue examined only a few islands or islands separated by extreme distances. In this study, we surveyed exotic and native plant diversity on 25 islands separated by <15 km in Boston Harbor. Exotic and native species richness were positively correlated. Consistent with island biogeography theory, species richness of both groups was positively related to area and negatively related to isolation. However, the isolation effect was significantly stronger for native species. This differential effect of isolation on native species translated into exotic species representing a higher proportion of all plant species on more distant islands. The community similarity of inner harbor islands vs. outer harbor islands was greater for exotic species, indicating that isolation had a weaker influence on individual exotic species. These results contrast with recent work focusing on similarities between exotic and native species and highlight the importance of studies that use an island biogeographic approach to better understand those factors influencing the ecology of invasive species.

Key words: biotic resistance; Boston Harbor Islands, Massachusetts, USA; dispersal; invasibility; invasive species; island biogeography; isolation; plant diversity; species richness; vascular flora.

INTRODUCTION

The influence of native species diversity on biotic resistance to invasion by exotic species remains unclear. In small-scale, manipulative experiments, the relationship between native species diversity and invasibility is typically negative (Stachowicz et al. 1999, Tilman 1999, Levine 2000, Naeem et al. 2000), suggesting that increased diversity can serve to deter exotic species invasions. At larger spatial scales, however, this relationship often reverses, yielding a positive correlation between native and exotic species diversity (Chown et al. 1998, Lonsdale 1999, Stohlgren et al. 1999, Sax et al. 2002). The reasons for this reversal (the invasion paradox sensu Fridley et al. 2007) remain unknown, but one possibility is that most communities are not saturated with species (Sax and Gaines 2008, Stohlgren et al. 2008) and both native and exotic species primarily respond to environmental factors other than species diversity across broad scales (Levine 2000, Fridley et al. 2007). Understanding why scale-dependent differences in diversity and invasibility emerge is critical if we are to better manage and conserve natural systems during a time of unprecedented exotic species introductions.

Islands provide a powerful setting for comparing the distribution and abundance of native and exotic species because variation in island size and isolation creates strong gradients in native species diversity that, in turn, may affect the distribution of exotic species (MacArthur and Wilson 1963, 1967). The equilibrium theory of island biogeography predicts that larger and less isolated (from mainland source populations) islands should support more diverse native communities. Interestingly, islands having these characteristics also tend to harbor high exotic species richness suggesting that they are functionally similar to other large, non-island areas where exotic and native species display positive relationships (Chown et al. 1998, Moody 2000, Sax et al. 2002, Russell et al. 2004).

Previous surveys of exotic and native species on islands have had two limitations. First, islands were often separated by large distances (>1000 km) and

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therefore differed markedly in their respective species pools. Second, within-archipelago surveys on smaller spatial scales (hundreds of kilometers) involved a limited number of islands and thus had limited statistical power (e.g., eight Channel Islands; Moody 2000). Low power limits the strength of conclusions based on nonsignificant relationships, such as the unexpected lack of an effect of isolation distance on exotic species richness (Moody 2000).

Here we present the results of a survey on the vascular flora of 25 islands within a temperate archipelago. Exotic and native species richness were correlated with environmental variables including island area, elevation, and isolation. We observed (1) a positive relationship between native and exotic plant species richness, (2) positive relationships with area and negative relationships with isolation for both groups, and (3) a strong differential effect of isolation on native vs. exotic species. Our results suggest that although exotic and native plants may respond to the environment in qualitatively similar ways, differences in their traits may ultimately influence their disparate distributions on islands.

Materials and Methods

The Boston Harbor Islands National Park Area (Boston, Massachusetts, USA) contains 30 islands that vary in size ($<$0.01–0.75 km^2) and isolation (0–6 km from the mainland). According to Wilson (2005), "the variation in area and in the degree of isolation of the islands in this miniature archipelago are ideal for close analysis of island biogeography." These islands are either outcrops of exposed bedrock or drumlins (i.e., elongate landforms of unconsolidated glacial tills) $<$40 m above sea level. Island soils are well-drained sandy loams formed from glacial till or outwash deposits.

In addition to gradients in size and isolation, these islands vary both in storm exposure and historical usage by humans. First, the outer islands (Calf, Graves, Great Brewster, Green, Little Brewster, Little Calf, Middle Brewster, and Outer Brewster) are more exposed to waves from oceanic storms. This exposure could influence species richness by modifying important soil characteristics such as salinity. Second, humans have used the islands for a variety of purposes for thousands of years, and this usage may have differed between islands. For example, the inner islands were probably used more heavily by Paleo-Indians (~8000 years ago) because of their proximity to the mainland (Richburg and Patterson 2005). However, by the end of the 17th century, most islands were inhabited, cultivated, and deforested (Richburg and Patterson 2005), and it is difficult to reconstruct the historical use of inner and outer islands.

Plant colonization of the Boston Harbor Islands occurred via three pathways. After the last glacial retreat, low sea level allowed colonization over land when the islands were connected to the mainland (Luedtke 1975). Later, as sea level rise isolated the islands from the mainland, subsequent colonization required that plants disperse across saltwater. Finally, humans intentionally and unintentionally introduced exotic species to the islands.

We surveyed the vascular flora on 25 of the 30 Boston Harbor Islands (see Appendix A for island details and Elliman 2005 for preliminary results). We omitted five islands because two are connected to the mainland via bridges and causeways (Long Island, Moon Island) and three were not surveyed due to logistical constraints (Shag Rocks, Gallops, and Hangman). Surveys were conducted during 62 field days in May–October of 2001–2003. Islands were visually surveyed to identify as many vascular plants on as many islands as possible and to search for rare plant species.

Surveys always included each of the dominant community types present on each island as determined from maps, aerial photographs, and previous surveys. Throughout the archipelago, we encountered the following habitats: brackish marsh, old fields, shoreline communities, shrub communities, woodlands, and forests. Although woodlands and forests are common on inner islands, these communities are absent on the outer islands perhaps as a result of storm exposure and the thin, rocky soils that limit tree establishment and growth. These outer islands tend to be dominated by sumac thickets and grass fields. A consequence of these habitat differences is that the canopy height on inner islands can exceed 15 m but rarely exceeds 3 m on outer islands. Shrubs commonly associated with sumac on inner islands, such as elderberry (*Sambucus canadensis*), raspberry (*Rubus idaeus*), bayberry (*Myrica pennsylvanica*), and viburnums (*Viburnum lentago*, *V. recognitum*, *V. trilobum*), are also scarce on the outer islands.

Large islands with diverse communities were visited repeatedly whereas small, depauperate islands were visited less frequently. On a per area basis, however, sampling effort on larger islands was less than that on smaller islands (Appendix B). Thus, the strong positive influence of island size on species richness that we observed would likely become stronger had we sampled the larger islands more extensively. All plant species encountered and growing without cultivation were identified. Samples were collected from individuals of unknown species and these were later identified in the laboratory (by T. Elliman) following the nomenclature of Sorrie and Somers (1999).

Island area measurements were obtained from Bell et al. (2002). The maximum elevation of each island was recorded (*available online*)[4] and island isolation was determined using the measure tool on GoogleEarth (*available online*).[5] For island isolation, we measured the shortest distance from vegetation on a given island to vegetation on the mainland. Because plants may use islands as stepping stones to disperse to more distant islands, we also calculated the step isolation, which we

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[4] ⟨www.usgs.gov⟩

[5] ⟨earth.google.com⟩

defined as the minimum distance a plant would have to disperse to reach the target island from the mainland using islands as stepping stones. To calculate step isolation, we measured the distance from each target island to the nearest mainland (a) and nearest island (b). If the target island was closer to another island than it was to the mainland (i.e., if a > b), thus making the other island a potential stepping stone for mainland-derived colonists, then we determined the distance from that stepping stone island to the mainland (c). To account for the possibility of multiple stepping stones, we also measured the distance from the nearest island to the island closest to the nearest island (d). If this distance was less than the distance from either the target island to the mainland or the nearest island to the mainland (i.e., if a > d or if c > d), then we used the shorter of the two distances (c or d) as the step isolation. For each target island, we repeated this procedure for nearby stepping stone islands until the distances from one of these stepping stone islands was greater than the distance from the target to the mainland. For Rainsford, Georges, and Lovells, the nearest island was Long Island, which is connected to the mainland by a bridge. Because the bridge on Long Island likely enhances human-mediated dispersal (humans and vehicles) that is absent on islands without bridges, Long Island was assumed to be part of the mainland when calculating step isolation for the five islands nearby.

We used simple linear regression to examine the relationships between several variables including exotic species richness, native species richness, island elevation, island area, and island isolation. For our species–area analysis, we compared $\log_{10}$(area) with $\log_{10}$(species richness + 1) because Graves, Little Calf, and Nixes Mate had zero native species. Although linear regression revealed no significant relationship between island area and isolation (linear regression, $R^2 = 0.03$, $P = 0.19$), indicating that there was no geographical bias in the distribution of large vs. small islands within the archipelago, we explored the effects of island isolation on native and exotic species richness independent of area effects. Hence, linear regressions of exotic and native species richness as a function of isolation were performed after adjusting for the effect of area. To do so, native and exotic species richness was $\log_{10}(x + 1)$-transformed, and island area was $\log_{10}$-transformed before fitting a linear model. The residuals yielded by this regression were then regressed as a function of island isolation for exotic and native species. To determine whether isolation effects differed for exotic and native species, we compared the slopes and y-intercepts of these two regressions using analysis of covariance. We also determined the nearest and furthest island that each plant species occupied, and calculated the difference between the isolation distances of these islands as an estimate of range for each species within the islands. The ranges were compared with a one-way analysis of variance that considered species type (exotic vs. native) as a fixed effect.

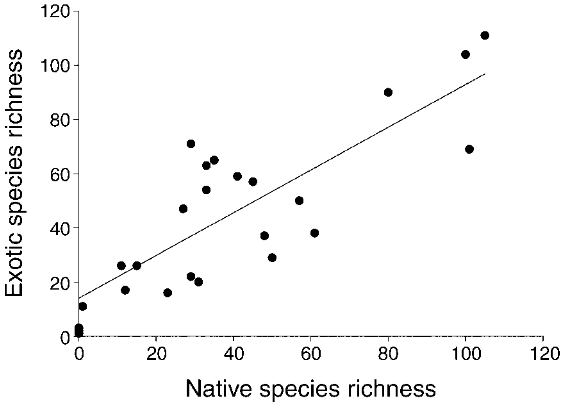

FIG. 1. The relationship between native and exotic vascular plant species richness by island in the Boston Harbor Islands, Massachusetts, USA ($N = 25$ islands). Each data point represents the total number of native and exotic species on an individual island. The fitted regression line is shown.

We observed different effects of isolation on native and exotic species. To test whether this pattern is related to differences in the ranges of single species within these groups (rather than changes in the identity of species with isolation), we compared the community similarities of the 17 inner and eight outer harbor islands. This division was based on isolation and exposure to oceanic storms. Outer islands included Calf, Graves, Great Brewster, Green, Little Brewster, Little Calf, Middle Brewster, and Outer Brewster. We calculated Jaccard's coefficient of community similarity for island pairs separately for either native or exotic species:

$$CC_J = c/(s_1 + s_2 - c)$$

where c is the number of species common to both islands and s is the number of species on each island. These pairwise comparisons were divided into the following contrasts: (1) each inner island with the other inner islands (inner–inner), (2) each inner island with the outer islands (inner–outer), and (3) each outer island with the other outer islands (outer–outer). Because Graves, Little Calf, and Nixes Mate had no native species, we were unable to calculate Jaccard's coefficient when comparing these islands with each other. For each comparison, we calculated a mean similarity and standard error for each island (inner–inner, $N = 17$ islands; inner–outer, $N = 17$; outer–outer, $N = 8$). We compared these similarities using three t tests with an alpha of $P = 0.016$ to adjust for multiple comparisons.

RESULTS

We identified 215 native and 202 exotic plant species. Two of these exotic plants, *Pyrus* sp. and *Rosa* sp., were not identified to the species level but are known exotics. An additional 42 plant species (~10% of all species) could neither be identified to the species level nor

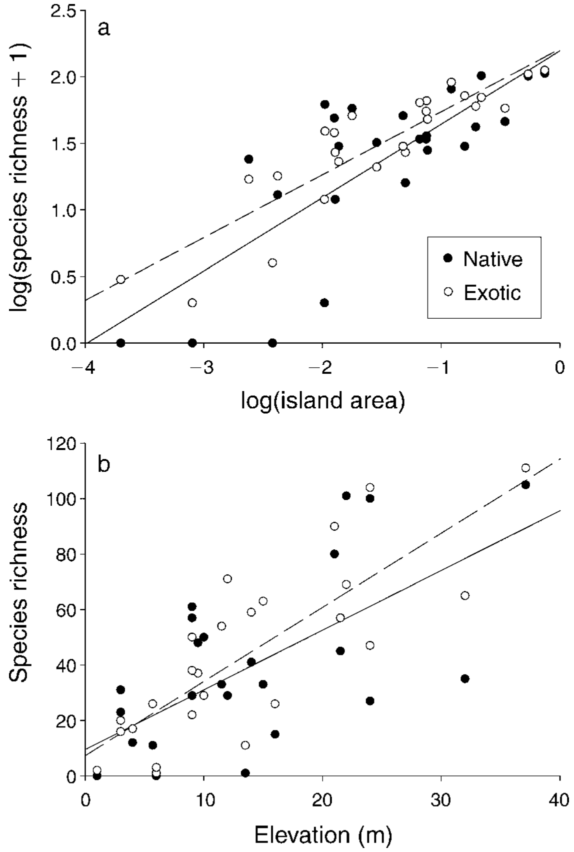

FIG. 2. The relationship between species richness and (a) area (originally measured in km^2) and (b) maximum island elevation for native and exotic vascular plants by island in the Boston Harbor Islands ($N = 25$). Fitted regression lines are shown (solid and dashed for natives and exotics, respectively). Within each graph, neither the slopes nor y-intercepts of regression lines were significantly different between native and exotic species (see *Results*).

designated as exotic or native and thus were excluded from our analyses. There was a strong, positive correlation between native and exotic vascular plant species richness on these islands (Fig. 1; exotic richness = 0.83(native richness) + 11.42, $R^2 = 0.70$, $P < 0.0001$).

Both native and exotic plant species richness were positively correlated with island area (Fig. 2a; log(native richness + 1) = 0.55log(island area) + 2.19, $R^2 = 0.58$, $P < 0.0001$; log(exotic richness + 1) = 0.47log(island area) + 2.21, $R^2 = 0.79$, $P < 0.0001$) and maximum island elevation (Fig. 2b; native richness = 2.15(elevation) + 9.49, $R^2 = 0.38$, $P = 0.0006$; exotic richness = 2.68(elevation) + 7.27, $R^2 = 0.63$, $P < 0.0001$). Furthermore, analyses of covariance revealed that there were no significant differences in the slopes or y-intercepts for each (native vs. exotic) regression pair involving island area or island elevation (ANCOVA: y-intercepts, all $P \geq 0.14$; slopes, all $P \geq 0.45$).

Species richness for natives and exotics decreased with increasing isolation from the mainland after controlling for the effects of island area (Fig. 3a; natives, $P < 0.0001$; exotics, $P = 0.0049$). However, native and exotic species differed with respect to the relationship between richness and isolation. Isolation explained more of the variation in native species richness (natives, $R^2 = 0.63$; exotics, $R^2 = 0.27$), and the negative effect of distance was much stronger (ANCOVA: $F_{1,46} = 10.61$, $P = 0.0021$) for native than for exotic species (natives: $y = -0.20x + 0.30$; exotics, $y = -0.07x + 0.20$). The differential effect of isolation on native and exotic species was also observed when we used the stepping stone isolation distances. Step isolation distances also explained more of the variation in native species richness (natives, $R^2 = 0.46$; exotics, $R^2 = 0.11$), and the negative effect of step isolation distance was significantly ($F_{1,46} = 7.17$, $P = 0.010$) stronger for native species than for exotic species (natives, $y = -0.37x + 0.32$; exotics, $y = -0.11x + 0.18$; graphs not shown). The proportion of all plant species that were exotic increased with increasing distance from the mainland (Fig. 3b; proportion exotic = 0.11(isolation) + 0.40, $R^2 = 0.76$, $P < 0.0001$).

Exotic species also spread more effectively to more distant islands. On average, the range of exotic species was 0.5 km greater than the range of native species (natives, 1.3 ± 0.1 km; exotics, 1.8 ± 0.1 km; $F_{1,415} =$

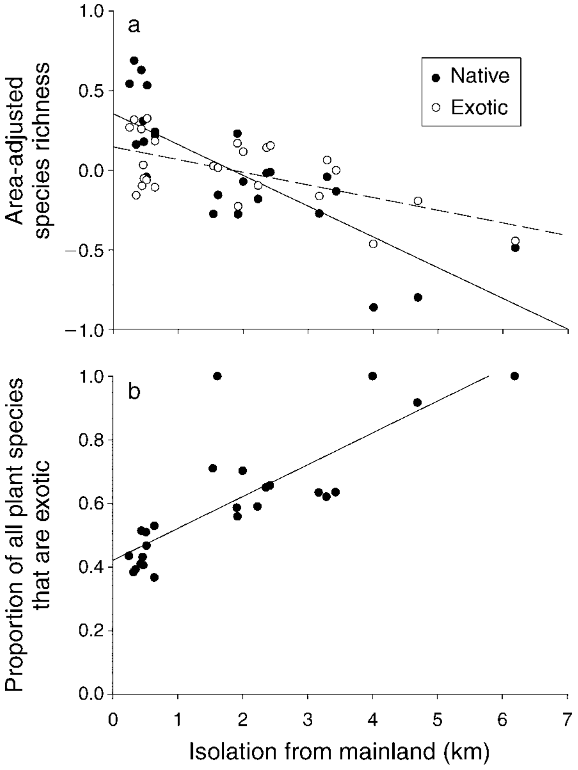

FIG. 3. (a) The area-adjusted species richness (i.e., the residuals from the species–area regressions) and (b) the proportion of all plant species that are exotic as a function of each island's isolation from the mainland (km). Data are reported on a per-island basis for the Boston Harbor Islands ($N = 25$). Fitted regression lines are shown (solid and dashed for natives and exotics, respectively).

3.864, $P = 0.002$). Community similarity between inner and outer islands was also greater for exotic than for native species (inner–outer, Fig. 4; $t_{2,32} = 4.15$, $P < 0.0001$) suggesting that the differential effect of isolation was at least partially the result of individual exotic species spanning a broader range than native species.

DISCUSSION

Despite the qualitatively similar effects of island area and isolation on both exotic and native species that were consistent with island biogeography theory, there was a much weaker effect of isolation on exotic species, and isolated islands contained a greater proportion of exotic species. Differential effects of isolation on native and exotic plants have also been reported for the Channel Islands (Moody 2000, Sax and Gaines 2005), suggesting that this pattern may be general for plants on archipelagos. Unfortunately, the Channel Islands are limited in number (eight islands used in Moody 2000), which restricts the ability of previous studies to detect differences between correlations for these islands (e.g., outliers can have a strong influence). We believe our data for 25 islands are less susceptible to this issue.

In contrast to recent reports that exotic and native species possess similar traits (Thompson et al. 1995, Meiners 2007), we observed differences in how these groups responded to isolation. For example, exotic species were better at becoming established on outer islands. Although the specific traits responsible for this pattern remain unknown, four hypotheses may explain it. First, exotic species may have greater dispersal capabilities. Second, humans may have dispersed exotics more often than natives. However, this hypothesis requires that humans utilized outer islands more heavily than inner islands. Although the historical use of the islands has not been well documented, the greater use of outer islands by humans seems unlikely. Third, exotic species may be more tolerant of the harsh environmental conditions encountered on the exposed, outer islands. In this case, exotic species may possess traits that reduce their extinction rates on outer islands. Finally, exotic species may be more successful on the more disturbed outer islands where mature forests and woodlands, which can act to prevent their establishment, are absent.

Recent evidence suggests that the relationship between exotic and native species depends on experimental scale. Although native species may competitively exclude exotic species at scales smaller than a few square meters, they appear incapable of doing so at larger scales where positive relationships between exotic and native species occur for such diverse groups as continental mammals (Sax and Gaines 2005), island birds (Sax et al. 2002, Sax and Gaines 2005), island plants (Moody 2000), and continental plants (Stohlgren et al. 1999, 2003). Consistent with these large-scale studies, we observed a positive relationship between exotic and native plant species in the Boston Harbor Islands that range in size from <0.01 to 0.75 km^2.

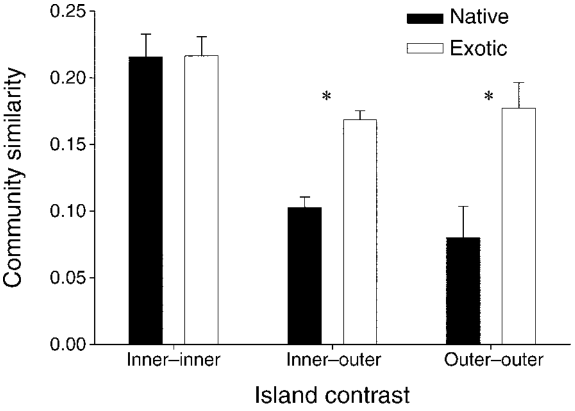

FIG. 4. Community similarity (Jaccard's coefficient, mean + SE) of islands based on either their native or exotic plant species richness. Inner islands were compared with each other ($N = 17$), and outer islands were compared with each other ($N = 8$). We also compared each inner island to the outer islands ($N = 17$). Asterisks denote significant differences ($P < 0.016$) between native and exotic species. Error bars indicate SE.

The two most likely mechanisms mediating the switch from a negative to a positive relationship between exotic and native species at larger scales are that both groups respond similarly to (1) environmental heterogeneity and (2) dispersal barriers such as isolation (Levine 2000). The environmental heterogeneity hypothesis posits that the negative effects (e.g., competition) of native species are overwhelmed by the positive effect of increased heterogeneity on exotic species: habitats with more niches are expected to support more species. The dispersal hypothesis argues that dispersal limits the ability of both groups to colonize isolated habitats at large scales but not at small scales. Hence, one expects the richness of both native and exotic species to be higher on near vs. far islands because both groups can more easily disperse to near islands. For example, the positive relationship Levine (2000) observed between native and exotic species richness at larger scales became negative when plots were experimentally seeded with exotic species propagules.

Our results suggest that both mechanisms are important to plants on the Boston Harbor Islands. The richness of both exotic and native species was strongly positively related to area and elevation, both of which are indirect measures of habitat richness (Fig. 2), thereby supporting the environmental heterogeneity hypothesis. However, species richness was also negatively correlated with isolation for both natives and exotics (Fig. 3a), which is consistent with the dispersal hypothesis. Thus, it is clear that these hypotheses need not be mutually exclusive. Obviously, exotic species and their invasion success will be influenced by their ability to disperse to new sites (propagule pressure) and, once there, by the environmental heterogeneity of the new habitat.

The qualitatively similar responses of exotic and native species to island area and isolation suggest that classic island biogeography theory may help explain the positive relationship of these plant groups on the Boston Harbor Islands. However, this theory cannot account for the much weaker effect of isolation on exotic vs. native species. Such differences may profoundly impact the invasibility of isolated habitats such as islands, especially when dispersal distances of exotics are similar to or greater than the isolation distances between habitats. When dispersal of both natives and exotics is greater than isolation distances, other factors should drive invasion success. Further comparative island studies should improve our understanding of the interactions between native and exotic species and our ability to conserve and manage those habitats where they increasingly co-occur.

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APPENDIX A

A table showing Boston Harbor Island characteristics, plant species richness, and proportional growth form (*Ecological Archives* E090-061-A1).

APPENDIX B

A figure showing that large islands were undersampled compared to small islands (*Ecological Archives* E090-061-A2).