

Species invasions on islands: searching for general patterns and principles

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Abstract Numerous islands worldwide are being increasingly invaded by exotic species. However, the effects of invading species on native floras remain underexplored, particularly whether island biogeography theory is applicable to native, exotic, and the newly assembled floras. Inter-group comparisons across different regions or island groups through a collection of individual studies have the potential of offering additional insights. Here, I comparatively analyze 10 datasets involving bird and plant invasions on nine island groups around the world and make detailed comparisons between two sets. I show that, although similarities exist, different taxonomic groups and different geographic settings exhibit drastically different invasion patterns on islands. Island biogeography theory still better explains native and overall (natives plus exotics) diversity patterns, such as the species-area-isolation relationships. In contrast, the corresponding patterns for exotic species are highly variable. The varying degrees of human intervention in species invasion relative to natural dispersal on different islands, along with differences between

taxonomic groups, highlight the challenges of searching general patterns and applying island biogeography theories to island invasion and conservation.

Keywords Area · Propagule pressure · Comparison · Degree of invasion (DI) · Isolation · Island biogeography

Introduction

The degree of invasions (DI) and invasibility of islands have been a central topic in invasion ecology and conservation biology (Vila and Ibanez 2011). However, to date, there is still little consensus on the methods for assessing DI and invasibility and interpretations of observed patterns. Among the heavily debated issues remains the invasibility of islands versus mainlands (Simberloff 1995; Sol 2000; Gimeno et al. 2006; Guo and Ricklefs 2010), mostly due to the high complexity involving both natural and human factors. Aside from many other possible factors related to intrinsic island features (Lomolino and Weiser 2001), a possible explanation could involve the relative roles of the geographic and human contexts of islands in research [i.e. the number of islands and their relative locations (e.g., Carstensen et al. 2012)] and continuing human influences after initial species introduction (Chown et al. 2005). This happens largely because most studies choose a set of islands (e.g.,

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continental vs. oceanic, sometimes in a particular region) and certain taxonomic groups for study (Kueffer et al. 2010).

The theory of island biogeography, which states that an island's species richness is a reflection of the balance between the colonization of new species and extinction of established species (MacArthur and Wilson 1967), has often been successfully applied to explain the patterns of natives, especially when the islands have not been substantially invaded by exotics (e.g., Whittaker and Fernández-Palacios 2007; Wu and Vankat 1995). It is less clear, however, whether the island biogeography theory could also be applied to explain the patterns of exotic species or all resident species when the islands studied have been heavily invaded. While finding general patterns of island invasions is desirable, identifying and explaining exceptions are equally critical for managing invasive species and allocating monitoring efforts. Evaluating the applicability of island biogeography theory to exotic species is essential, yet it is equally important to know whether the theory still applies to native species assemblages, which might have been greatly altered due to past, ongoing, and even accelerating species invasions expected in the future. Comparative studies are especially helpful in this regard because they allow for additional analyses without the collection of additional data and are able to offer additional insights behind the observed patterns found through the individual investigations (Daehler 2006). Although intrinsic island features such as area and isolation could potentially affect invasion, other possible explanations for different results observed on different (sets of) islands require in-depth investigation (Sax et al. 2002).

Due to the growing impacts of exotic species, recent studies have significantly advanced our understanding of species invasions in island ecosystems (Blackburn et al. 2008; Kueffer et al. 2010). However, comparisons among studies to date continue to highlight the challenges in searching for general patterns and applications of island biogeography theories in island invasion and conservation (Sol 2000; Kueffer et al. 2010). In order to gain valuable insight on patterns of biotic invasions on islands related to the applicability of island biogeography principles, in this study I comparatively examined 10 datasets compiled in recent studies on bird and plant invasions on nine groups of islands (Table 1) in

relation to geographic locations, relative human influences, invasion pathways, and the dispersal mechanisms (e.g., Duncan et al. 2003; Li et al. 2006). I also performed additional analyses on: (1) the native-exotic species richness relationships, (2) the species-area-isolation relationships that include all species (i.e., natives and exotics combined), and (3) the relationships between DI (measured by exotic fraction or proportion of exotic species in the community) and island features, such as island area and isolation. I then make much detailed comparisons between two recent case studies on birds versus plants (i.e., Blackburn et al. 2008 and Long et al. 2009), with most contrasting island features and patterns of invasion (Tables 1, 2; Fig. 1). In all analyses, simple linear and nonlinear regressions were conducted. I hypothesize that, because of the human factors and time limits in species invasions, the island biogeography theory would still be more applicable on native than on exotic species (Kueffer et al. 2010).

General comparisons of species-area-isolation relationships

The comparative results based on the 10 datasets of island invasions by birds and plants shown in Table 1 were based on six recent studies. Two of the datasets were compiled by Sax et al. (2002), which included only oceanic islands around the world with permanent human inhabitants (23 involving bird invasion and 13 plant invasions after human settlement). Another dataset was compiled by Chown et al. (1998) in an examination of bird, plant and insect invasions on 25 southern ocean islands. Unlike the islands examined by Blackburn et al. (2008), only 11 of the 25 islands were occupied by humans, and some not permanently. The dataset by Kueffer et al. (2010) included plant invasions on both oceanic and continental islands or island groups (No. = 30) also inhabited by humans. Walsh et al.'s (2012) dataset included 65 continental and oceanic islands, from which richness data of native and exotic birds, amphibians, and mammals were collected, and information on European settlement, human population density, and number of major ports was available. The datasets compiled in this study also included both oceanic and continents islands with human inhabitants (No. = 34 for birds and No. = 44 for plants; Table 1). Details of the

Table 1 Comparisons of correlation coefficients (*r*) in the species-area-isolation relationships of plants versus birds on different sets of islands around the world

No. islands	Taxa	Native-exotic relation	Area (km ²)			Isolation (km)				
			Native		Exotic		Native		Exotic	
			All species	Exotic	All species	Exotic	All species	Exotic	All species	Exotic
Blackburn et al. 2008	Birds	0.38*	0.79**	0.08	0.72***	-0.17	-0.06	0.81*	0.01	0.45*
Sax et al. 2002 [§]	Birds	0.27	0.76***	0.50*	0.79***	-0.47**	-0.33	0.03	-0.84***	0.48**
Chown et al. 1998	Birds	0.45*	0.25*	0.11	0.44*	-0.00	-0.21*	0.48**	-0.74***	0.24
Walsh et al. 2012	Mixed [†]	0.35*	0.75***	0.31*	0.71***	-0.36*	-0.37*	0.30*	-0.18	0.52***
This study	Birds	0.46*	0.85***	0.15	0.85***	-0.66**	-0.44*	0.37*	-0.45*	0.54**
Chown et al. 1998	Plants	0.68***	0.38**	0.50**	0.65***	0.47*	-0.15	-0.03	-0.23	0.27
Sax et al. 2002 [§]	Plants	0.98***	0.88***	0.91***	0.90***	-0.03	-0.15	0.13	-0.14	0.03
Long et al. 2009	Plants	0.84***	0.77**	0.89***	0.75***	-0.39†	-0.53*	-0.41*	-0.50*	0.84***
Kueffer et al. 2010	Plants	0.73***	0.54**	0.70***	0.78***	-0.65***	-0.49*	-0.19	-0.47**	0.50**
This study	Plants	0.08	0.67**	0.34	0.60**	-0.71**	-0.34	-0.30	-0.39†	0.57**

All data except exotic fraction were log-transformed (where species richness = 0 in any dataset, the richness data were log [n + 1] transformed)

[§] Island isolation data added in this study; * *p* < 0.05, ** *p* < 0.001, *** *p* < 0.0001; † Including birds, amphibians, and mammals

[†] Marginally significant (0.05 < *p* < 0.1); Values in roman, italic, bold and bold italic indicate that the findings are in total agreement, agreement but not significant, disagreement but not significant, and total disagreement with the island biogeography principles, respectively

Table 2 An example showing that different sets of islands and/or taxonomic groups (Fig. 2) can lead to different conclusions of biotic invasion patterns

	Blackburn et al. (2008)	Long et al. (2009)
<i>Island features and organisms</i>		
No. islands	35	25
Location	Worldwide	Boston Harbor
Distribution	Scattered	Clustered
Origin	Oceanic	Continental
Area (km ²)	Large (17–5.87 × 10 ⁵)	Small (0.01–0.75)
Distance to mainland (km)	Far (90–3,700)	Close (0.25–6.19)
Organism	Birds	Plants
Exotic species definition	Each island	New England
Human population	Residents (34 islands)	Camping (3 larger islands)
<i>Partial invasion mechanisms</i>		
Pathway of species introduction	100 % human	Human + natural dispersal
Secondary dispersal	Absent	Present

+ Including both natives and exotics

island groups examined by Blackburn et al. (2008) and Long et al. (2009) are provided in Table 2.

Comparisons of results among the 10 datasets from nine groups of islands around the world showed that, although similarities exist, different taxonomic groups and different geographic settings exhibit different invasion patterns on islands (Table 1). In all 10 datasets, the native-exotic richness relationships were positive, but two were non-significant (i.e., the bird data in Sax et al. 2002 and plant data compiled in this study).

The native species, and even overall (natives and exotics) species richness, appeared to follow the island biogeography principles better than exotic species. In all cases, native species richness and overall species richness increased with area. On the other hand, for exotic species, only 5 out of 10 cases showed significant increase in richness with area, despite the fact that in all cases the species-area relationships were positive. Additionally, all 10 species-isolation relationships for native species were negative, yet 6 out of 10 were positive for exotic species, especially for birds.

In general, area exhibited greater explanatory power than isolation. For example, among the 30

species-area relationships (Table 1), only four were non-significant. In contrast, among the same number of species-isolation relationships, 12 were non-significant. Most of the deviations from the species-area-isolation relationships predicted by the island biogeography theory, i.e., no correlations or opposite correlations observed in this synthesis, were found in exotic birds, suggesting that island biogeography theory is more applicable to exotic plants than to exotic birds. For example, the species-isolation relationships were negative in three out of four cases for exotic plants, but were positive in all four cases for exotic birds (i.e., against the island biogeography principles; Table 1).

Detailed comparisons between two case studies

Analyzing islands in a particular region, or collectively from around the world, are two commonly adopted methods in island biogeography. Two recent studies that show contrasting patterns of bird and plant invasions require a closer comparative examination in order to better understand the differences observed between the patterns of these two taxonomic groups (the details of each study are provided in Table 2). On a global scale, Blackburn et al. (2008) studied bird invasions on 35 oceanic islands around the world that are remote from any continent and from each other; On

a much smaller scale, Long et al. (2009) studied plant invasions on 25 continental islands in Boston Harbor that are close to each other and to the mainland (Fig. 1).

A detailed cross-taxa comparison between these two case studies reveals contrasting patterns between birds and plants that could be linked to geographic setting and context and dispersal. Consistent with the general theory of island biogeography (MacArthur and Wilson 1967; Wu and Vankat 1995; Whittaker and Fernández-Palacios 2007; Clark et al. 2011), both Blackburn et al. (2008) and Long et al. (2009) report positive species-area relationships for native and exotic species. When both native and exotic species are combined, the overall species-area relationships were also strong (Fig. 2a, b). Furthermore, the combined bird richness exhibited an increasing trend (non-significant), but the combined plant richness declined with isolation for plants (Table 1; Fig. 2c, d).

The most striking finding from this comparison was the contradictory effect of isolation on exotic richness: a positive isolation-exotic richness relationship was found in Blackburn et al. (2008), while a negative relationship was found in Long et al. (2009) (Fig. 3a, b). The former also reported no area-exotic fraction relationship, while the latter found a negative relationship. Positive relationships between isolation and exotic fraction were observed in both studies (Table 1; Fig. 3c, d).

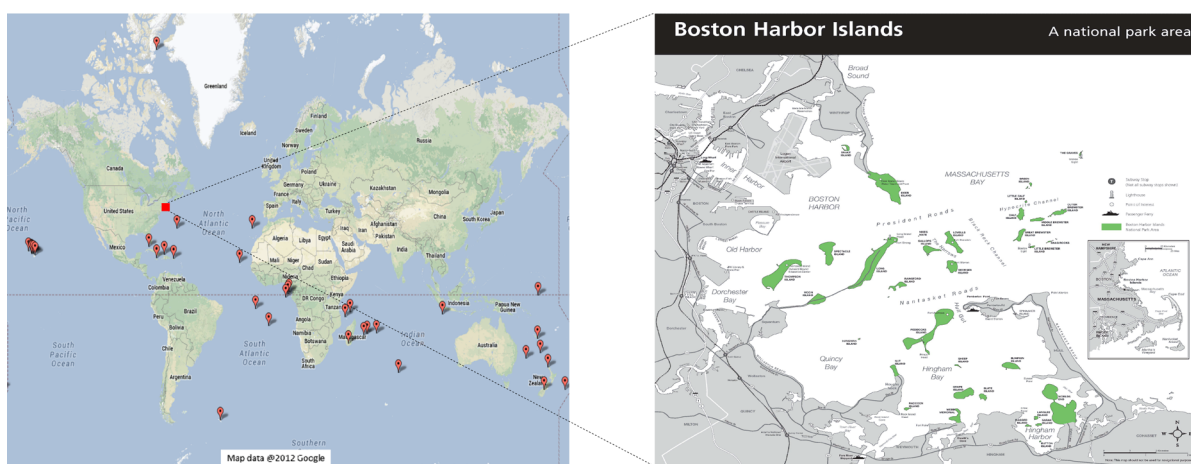


Fig. 1 Comparison of geographic settings between the two sets of islands examined by Blackburn et al. (2008; 35 world islands in red—left; made using Google Map) and Long et al. (2009; 25

Boston Harbor islands in green—right; adopted from <http://www.nps.gov/boha/historyculture/upload/Park%20Map.pdf>). (Color figure online)

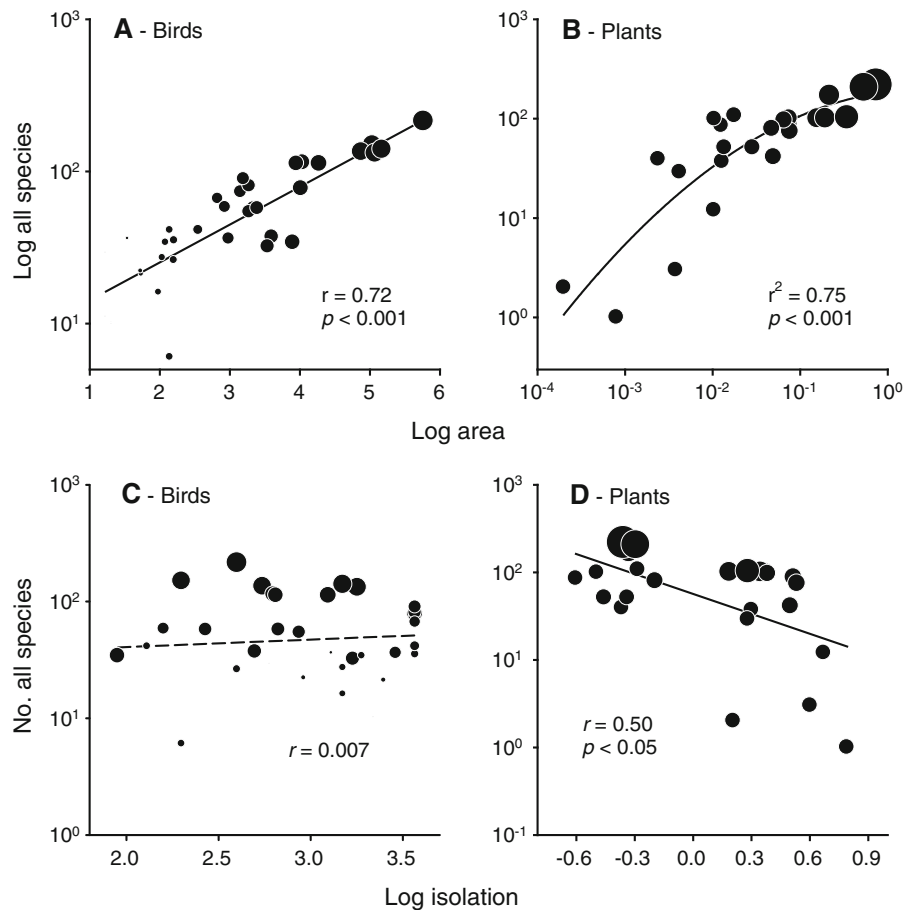


Fig. 2 Species-area relationships for both birds (a) and plants (b) are much stronger when all (natives and exotics) are combined than when either native or exotics only are used for both sets of islands examined by Blackburn et al. (2008) and

Long et al. (2009). In contrast, birds (c) and plants (d) show very different species-isolation relationships in the two independent studies. Symbol size represents relative isolation among islands examined in each study

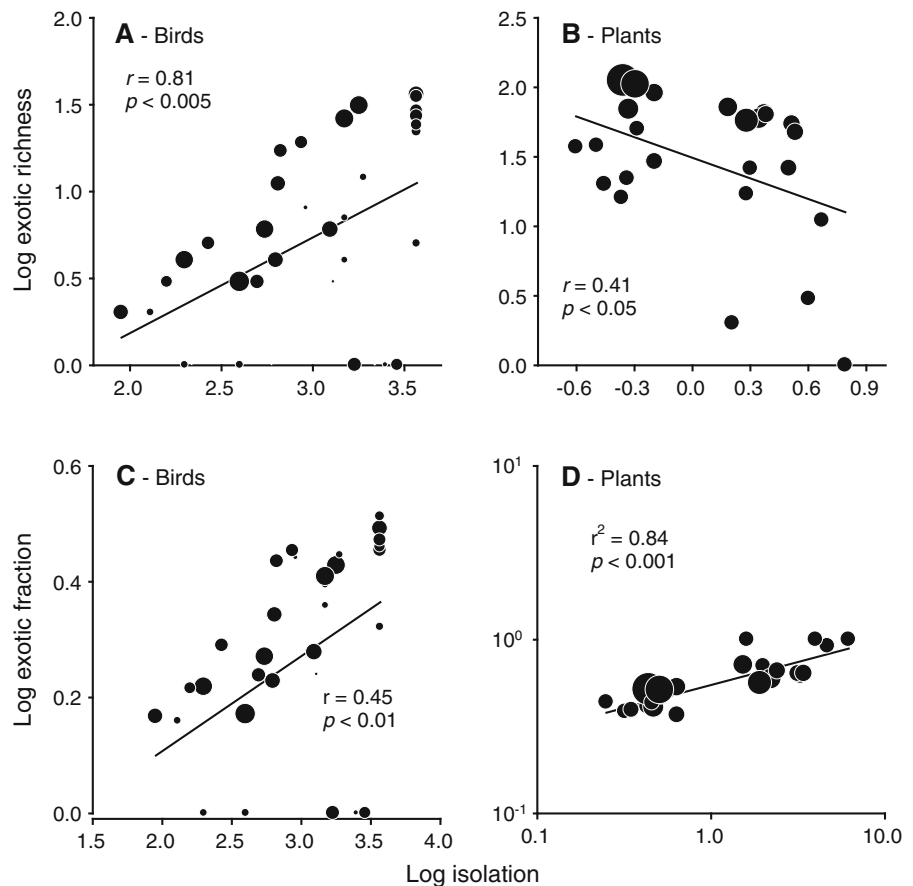
Mechanisms and implications

The broad comparisons among the 10 datasets combined with the detailed comparison between the two most recent studies clearly show that patterns of species invasion on islands are often context- and taxon-dependent. In spite of similarities in native species-area relationships, different taxonomic groups or sets of islands could present drastically different island invasion patterns. In general, the species-area-isolation patterns for exotic species are highly variable, especially for animal groups (Table 1), depending on the relative roles of human versus natural dispersal and geographical contexts (e.g., the number and location of islands). For the human factor alone, the relative role of intentional and unintentional

introductions could determine the invasion outcomes (see below).

The analysis considering all resident species (natives plus exotics) together may have important implications. It may highlight the higher overall diversity on islands resulting from the increased saturation level due to the addition of exotic species (Terborgh and Faaborg 1980). This analysis may also stress critical questions in ongoing research or monitoring such as: (1) whether invaded species are complementary with resident species in terms of resource use; (2) whether increased diversity could help resist further invasions by other species; (3) whether the increased diversity is transitional (i.e. only existing in the short-term) or sustainable over the long-term., and (4) whether the invaded species could

Fig. 3 Contrasting relationships between isolation and exotic richness on islands; i.e., positive for birds (a, modified from Blackburn et al. 2008) and negative for plants (b, modified from Long et al. 2009). However, for both birds (c) and plants (d), DI or exotic fraction increases with isolation. *Symbol size* represents relative island area among islands examined in each study (log-transformed)



achieve dominance or become highly abundant, thus leading to local extinction of rare natives or even invaded species with small populations (Sax et al. 2002). The lack of native species-isolation relationship and the strong positive exotic species-isolation relationship in Blackburn et al. (2008) and some other cases in Table 1 could indicate the possibility of extinctions of native birds on more remote islands due to competition from introduced species.

What could cause the seemingly conflicting results listed in Table 1 and between the two studies by Blackburn et al. (2008) and Long et al. (2009), especially the opposite effect of isolation on exotic richness? First, birds and plants have different dispersal mechanisms and experience very different pathways of exotic species introductions. Bird introductions to the remote oceanic islands may largely rely on human intentional introduction and relatively more species might have been introduced to more remote and isolated islands where native species richness is low (Blackburn et al. 2008). Such introductions often

have excellent records. In contrast, there is no evidence of a tendency of people to introduce more plant species to relatively more remote islands of the 25 islands in Boston Harbor. Instead, the colonization of exotic plants to the nearby islands is facilitated by both intentional and accidental introductions by humans.

Overall, natural dispersal may play a greater role in plant colonization on uninhabited islands close to each other and to the mainland, relative to more remote inhabited islands (Blackburn and Duncan 2001; Kueffer et al. 2010). The different dispersal characteristics associated with birds and plants could be a major factor controlling the exotic species-area-isolation patterns (Pyšek and Richardson 2006). For example, among the remotely isolated islands (i.e. from the mainland and among each other; Fig. 1) studied by Blackburn et al. (2008), natural dispersal is less likely; but for plants on islands in Boston Harbor, the significant movement of viable seeds facilitated by both natural and human dispersal must have followed

from the initial introduction of exotic species to the mainland New England area (Allen et al. 2013) and further to the nearby islands. In such invasions, the process is always more complicated as it involves both human and natural dispersal factors and their relative contributions are often difficult to determine. Thus, the more remote islands studied by Long et al. (2009) would undoubtedly suffer smaller propagule/colonization pressure and therefore have lower exotic richness and fraction.

As in most, if not all, field studies of plant invasions, it is virtually impossible to separate the contribution of natural dispersal (i.e. after the plants have been introduced to nearby areas) from that of human introduction. The islands examined by Long et al. (2009) are small, close to each other and to the mainland, and most of the islands are not inhabited, thus deliberate human introductions are less likely in these islands (Note: This is very different from the larger islands examined by Kueffer et al. 2010 with human residents who might have intentionally introduced many plants species from other places, which is similar to Blackburn et al.'s 2008 observation that human intentionally introduced more birds to remote islands where they inhabit). Furthermore, there are usually more native than exotic woody species on the same island, but more exotic than native herbaceous species (Long et al. 2009). Although exceptions exist, herbaceous plants usually have many more seeds, albeit smaller, than woody plants, thus exhibiting greater dispersal abilities that promote their occupation on more isolated islands (Rejmánek and Richardson 1996; Richardson et al. 2000; Ricklefs et al. 2008). However, other factors may be involved as well such as human-mediated dispersal (accidental movement of smaller seed on vehicles, boats, and clothing) and better survival of such seeds on the remote islands.

Second, the naturalization of exotic species depends on geographical context. The two sets of islands compared in detail are located in very different geographic settings, as reflected by the different sizes and isolation levels (Fig. 1). The oceanic islands studied by Blackburn et al. (2008) are generally larger, highly isolated from the mainland and from each other, and most have human residents. In contrast, the Boston Harbor Islands are much smaller, close to mainland and each other, and have no human residents (Table 2). The relatively short distances among Boston Harbor islands may pose strong neighborhood

effects (i.e. species turnovers among islands) (McKinney 2005), while the more isolated islands examined by Blackburn et al. (2008) would not experience such effect (Fig. 1).

Recognizing the drastic differences between types of organisms is critical for identifying and explaining the spatial and temporal patterns of species invasion and naturalization. Similar to unique traits and natural history of individual species, not only do different species groups exhibit quite different phylogenetic history, but for various reasons, they also experience drastic different influences from humans (e.g., human assisted dispersal or migration, introduction records and pathways). Similarly, different sets of islands chosen for study would also be likely to exhibit different patterns depending on their unique contexts such as location, geographic arrangement, number, size, and isolation. Yet, despite the seemingly opposite isolation-exotic richness relationships in the two studies, the DI is mainly determined by the relative role of human intervention (e.g., pathways) versus natural dispersal (Gillson et al. 2008; Lockwood et al. 2009), which varies with geographic and human contexts. Likewise, it is important to recognize the similarities among studies, especially those that can be readily explained by well-established ecological theories. For example, physically, in both sets of islands, the ones closer to continents tend to be either small or big and numerous, whereas the isolated ones tend to be small and few (Fig. S1). Therefore, the area and isolation are somewhat related to one another and could jointly affect the results and conclusions. Also, when both natives and exotics are combined in consideration, much of the commonalities in the two studies may be explained by the island biogeography theory.

Third, as shown above, different measures such as exotic richness, exotic fraction, and abundance could lead to different and sometimes contradictory conclusions in terms of DI and invasibility (Sax et al. 2002), thus should be treated with considerable caution. On the other hand, results from different measures could nonetheless offer additional insights on the mechanisms of species invasions. In the two-study comparison, Blackburn et al. (2008) showed no effect of area on exotic fraction, despite the positive area-exotic richness relationship; while Long et al. (2009) showed that isolation has a positive effect on exotic fraction but a negative effect on exotic richness. Data by Chown et al. (1998) is even more puzzling, as they

show a positive effect of area on exotic fraction, which is a totally opposite pattern from all other studies in Table 1 (see also Guo and Ricklefs 2010; Guo and Olden 2014). Clearly, there is a shift in relative importance of native richness with isolation and in the role of human introduction in invasion patterns between the two studies. Furthermore, the comparison between birds and plants on islands also raises an interesting but highly challenging issue: how to count ‘exotics’ when secondary dispersal is heavily involved but there is no introduction record (Rodriguez-Cabal et al. 2013). Blackburn et al. (2008) use the oceanic islands themselves to define exotics, while exotic plants on Boston Harbor Islands are defined as those exotic to the New England region (J. Long and T. Elliman, personal communications; see also Guo and Ricklefs 2010). However, it is unlikely that this difference would significantly alter the comparative results between the two studies.

Finally, it is unfortunate that I could not examine the possible effects of spatial heterogeneity and landscape pattern within the studied islands on invasion patterns by different taxonomic groups (i.e., residues or deviations of data point or islands from the regression lines in Figs. 2 and 3) due to limited data. The patterns found in selected studies for comparisons listed in Table 1 are by no means representative of species invasions on islands, and findings from each study must be interpreted on a case-by-case basis. For example, even for the same taxonomic group, birds, Chown et al.’s (1998) data exhibited negative although not significant species-isolation relationship, whereas Blackburn et al. (2008) showed the opposite (Table 1). This was at least partially due to the fact that only some of the islands examined by the former were occupied by humans and some were only semi-permanently, but those by the latter were all occupied by permanent human residents. Additional research is clearly needed in the future to address the important issues related to habitat heterogeneity and land use on the islands to fill the critical information/knowledge gap (Vila and Ibanez 2011; González-Moreno et al. 2013; J. Wu personal communications).

Conclusions

Results from this synthesis support my hypothesis that the island biogeography theory is still more applicable

to native species than to exotic species. However, given the accelerating biotic invasions and their growing impacts on native species, whether such pattern may persist over time remains to be seen. The patterns of biotic invasions on islands vary greatly among taxonomic groups associated with specific pathways of species introductions and dispersal and among island groups (e.g., location, type) with different human impacts (Lockwood et al. 2009; Cassey 2009; Blackburn et al. 2013; Dawson et al. 2013). Comparisons among individual case studies add new insights regarding the relative role of geographic and human contexts in island invasions by different taxonomic groups. Nonetheless, caution is always needed in describing and interpreting patterns of species naturalization on islands, especially when making generalizations. More comprehensive comparative studies among world islands are needed in the future.

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