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Invasibility of tropical islands by introduced plants: partitioning the influence of isolation and propagule pressure

Invazibilita tropických ostrovů: vliv izolace a tlaku propagulí

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All else being equal, more isolated islands should be more susceptible to invasion because their native species are derived from a smaller pool of colonists, and isolated islands may be missing key functional groups. Although some analyses seem to support this hypothesis, previous studies have not taken into account differences in the number of plant introductions made to different islands, which will affect invasibility estimates. Furthermore, previous studies have not assessed invasibility in terms of the rates at which introduced plant species attain different degrees invasion or naturalization. I compared the naturalization status of introduced plants on two pairs of Pacific island groups that are similar in most respects but that differ in their distances from a mainland. Then, to factor out differences in propagule pressure due to differing numbers of introductions, I compared the naturalization status only among shared introductions. In the first comparison, Hawai'i (3700 km from a mainland) had three times more casual/weakly naturalized, naturalized and pest species than Taiwan (160 km from a mainland); however, roughly half (54%) of this difference can be attributed to a larger number of plant introductions to Hawai'i. In the second comparison, Fiji (2500 km from a mainland) did not differ in susceptibility to invasion in comparison to New Caledonia (1000 km from a mainland); the latter two island groups appear to have experienced roughly similar propagule pressure, and they have similar invasibility. The rate at which naturalized species have become pests is similar for Hawai'i and other island groups. The higher susceptibility of Hawai'i to invasion is related to more species entering the earliest stages in the invasion process (more casual and weakly naturalized species), and these higher numbers are then maintained in the naturalized and pest pools. The number of indigenous (not endemic) species was significantly correlated with susceptibility to invasion across all four island groups. When islands share similar climates and habitat diversity, the number of indigenous species may be a better predictor of invasibility than indices of physical isolation because it is a composite measure of biological isolation.

Keywords: invasion, islands, Fiji, Hawaii, naturalization, New Caledonia, Pacific, pests, Taiwan

Introduction

The invasibility of a habitat, ecosystem or region can be defined as the area's overall susceptibility to invasion (Williamson 1996). Much attention has focused on describing regional and ecosystem-level patterns of invasibility or resistance (the converse of invasibility) through comparative studies of alien floras (e.g. Rejmánek 1989, Rejmánek 1996). Such studies have lead to substantial insights that have inspired ongoing theoretical developments and experimental research in invasion biology (Pauchard et al. 2004, Pyšek et al. 2004). For example, temperate regions appear to be more susceptible to invasion than tropical regions

(Rejmánek 1996, Lonsdale 1999), some biome types such as savannas and deserts appear to be less susceptible to invasion than others (Lonsdale 1999), and islands are generally more susceptible to invasion than mainlands (Lonsdale 1999, Denslow 2003).

In regional studies, the number of non-native species naturalized in an area is commonly used as a measure of invasibility. Larger areas may experience more species introductions and have greater habitat heterogeneity, so invasibility is often expressed as the number of naturalized species per unit area or per native species, where the number of native species is used as a surrogate for area (Rejmánek 1996, Lonsdale 1999). Yet, native species might also have a direct influence on invasibility by providing biotic resistance to invaders (Mack 1996, Rejmánek 1998). Although there is little direct evidence that biotic resistance shapes regional-scale patterns of plant naturalization (Levine & D'Antonio 1999, Daehler 2001a, Rejmánek et al. 2004), simple lottery models, assuming only variation in growth rates among species, suggest that communities assembled from smaller species pools will be more susceptible to invasion than communities assembled from larger species pools (Herben 2005).

The number of species that naturally reaches an island is expected to decrease with increasing distance from a mainland source pool. This effect can be due to decreasing rates of immigration to more distant islands (MacArthur & Wilson 1967), but species also have inherent differences in dispersability, resulting in arrival of a non-random subset of the mainland species pool. Because of the sampling effect imposed by distance, the biotas of more isolated islands tend to be derived from smaller pools of colonists, and therefore they can be expected to be more vulnerable to invasions, all else being equal (Herben 2005).

Besides the influence of a limited pool of natural colonizers on invasibility, the number of human-facilitated introductions to a region, or propagules pressure, also affects the number of naturalized species (Williamson 1996, Colautti et al. 2006). Propagule pressure is usually ignored in regional assessments of invasibility because it is difficult to know how many species have been introduced to an area (Lonsdale 1999). Some, or perhaps most reported variation in invasibility among regions, sites or islands can probably be accounted for by variation in propagule pressure, rather than differences in invasibility per se (Rejmánek 1996, Rejmánek 1998)

A final factor that can influence estimates of invasibility is variability in the criteria used to determine which species are counted as naturalized or invasive. Most issues relating to the whether individual species are native or introduced to an island can be worked out by examining historical records and biogeography. But even after the introduced species have been determined, the number of naturalized or invasive species depends on definitions, which often vary among data sources (Pyšek et al. 2004). Invasion is a sequential and selective process consisting of various nested stages (Lockwood et al. 2006), and these stages proceed along a continuum, rather than in truly discrete steps (Richardson et al. 2000). Among any pool of introduced species, some of them will at least occasionally escape from the point of introduction or planting; a subset of those that escape will establish long-lived populations, and a still smaller subset will spread widely into the surrounding areas. Finally a few of these species will become pests (Williamson 1996), a designation that is usually reserved for species that have substantial, unwanted impacts from a human perspective. Richardson et al. (2000) proposed standard criteria for determining which species are casual, naturalized, or invasive, but it can be difficult to precisely assign species to these categories based on information provided by floras and other readily available data sources (Pauchard et al. 2004, Pyšek et al. 2004). Most studies comparing invasibility of different areas have ignored the degree to which introduced species have been able to invade, even though this information can provide us with a better understanding of invasion patterns (Pyšek et al. 2004) and allow better assessments of the expected impacts of introduced species (Ortega & Pearson 2005).

In this study, I examined the hypothesis that remote islands are more susceptible to invasion than islands closer to a mainland, based on the assumption that remote island biotas are derived from a smaller pool of colonists (Herben 2005). I compared two pairs of Pacific island groups that are similar in most respects, except for their distance from a mainland species pool: Hawai‘i and Taiwan, and Fiji and New Caledonia (Fig. 1, Table 1). All four of these island groups are located at similar tropical/subtropical latitudes (either north or south of the equator), and they are all high islands, with mountains >1000 m in elevation. Hawai‘i and Taiwan share climatic zones ranging from warm tropical lowlands to alpine mountaintops. New Caledonia and Fiji share ecological zones from tropical lowlands to cool montane cloud forests. Thus, the available habitats for invasion are similar within each paired island group. These island groups are also similar in physical area (Table 1).

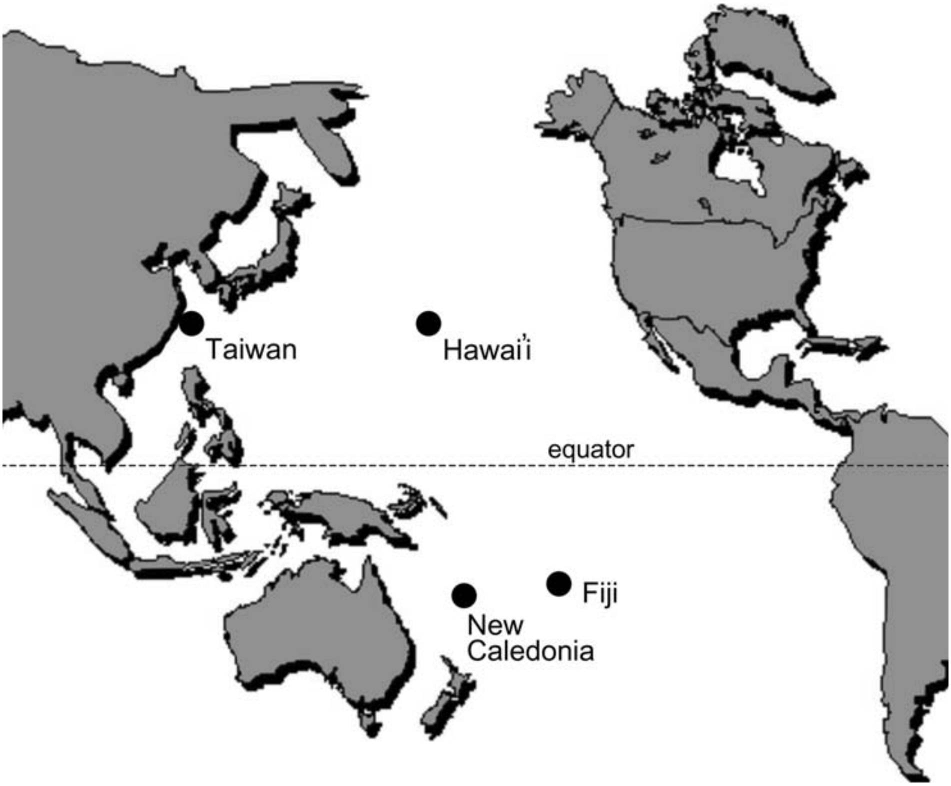

Fig. 1. – Map of the Pacific Ocean, showing the locations of paired island groups (Hawaii and Taiwan, Fiji and New Caledonia) relative to mainland continental regions.

Table 1. – Some key features of the island groups compared in this study.

Region	Latitude	Approx. distance from mainland (km)	Area (km^2)[1]	Highest elevation[1]	Human population density (per km^2)[1]	Endemic species	Native but not endemic
Hawai'i	21°N	3700	16,580	4,200	66	850[2]	106
Taiwan	23°N	160	32,260	3,952	709	750[3]	2650
Fiji	18°S	2500	18,270	1,324	48	475[4]	827
New Caledonia	21°S	1000	19,100	1,628	11	2320[4]	681

[1] CIA worldfact book 2006 (http://www.cia.gov/cia/publications/factbook); [2] Wagner et al. (1999); [3] Based on 3400 species total as summarized in Hseih et al. (1993) and an endemism rate of 22% estimated by Peng and Yang (1992); [4] Jaffré et al. (2001)

To make an initial assessment of invasibility, I examined the number of non-native plant species that had reached each of three sequentially smaller, nested species pools corresponding to different stages of the invasion process: escape (all casual plus naturalized species), naturalization (naturalized species only), and pest species (a subset of naturalized species). Then, to factor out differences due to propagule pressure caused by different numbers of species introductions to each island group, I compared success rates only among the species that had been introduced to both islands in a pair. As a second measure of invasibility, I also calculated the probability of a species naturalizing or becoming a pest in the remote islands, given that it had done so in islands closer to a mainland, and vice versa. Based on the species sampling hypothesis, island invasibility should decrease with an increasing number of natural (native) colonists (Herben 2005). Although other studies have examined relationships between total native species richness and invasibility (e.g. Lonsdale 1999), total native species richness is not a good estimator of the number of independent island colonists because adaptive radiations, which are common on islands, can dramatically inflate the number of native species. In contrast, the number of non-endemic indigenous species is expected to be positively related to island colonization rates; therefore, to test predictions of the species sampling hypothesis (Herben 2005) across all four island groups, I tested for a negative relationship between native (but not endemic) species richness and naturalization rates among plants introduced to all four island groups.

Materials and methods

In this paper, I consider invasion to be a process during which an introduced plant becomes established and then spreads outside its native range, with some of these species becoming pests (Williamson 1996). I consider a species to be naturalized when it reproduces regularly without direct human assistance, and when it has established sustained populations over several lifecycles (Richardson et al. 2000). In contrast, casual species are those that have been observed growing outside of cultivation, but they have not established persistent populations over many lifecycles (Richardson et al. 2000). I consider weakly naturalized species (those not meeting the above criteria for naturalization) in the same category as casuals because they are not reliably distinguished from casuals based on occurrence data, and there is no definitive line between casual and weakly naturalized stages in the invasion process. Pest species are naturalized species that have been reported as having unwanted ecological or economic impacts. I chose not to categorize individual species as 'invasive' to avoid confusion or controversy over the use of this term as a species descriptor (Davis & Thompson 2000, Richardson et al. 2000, Daehler 2001b). The status of introduced plants in each island system was determined based on the available literature using comparable, though not identical criteria, since the available information differed somewhat for each island system.

For Hawai'i, species were considered naturalized when Wagner et al. (1999) described the species as naturalized in general terms on at least one island, or when the species was reported as naturalized from at least three separate localities. The latter criterion is similar to that used by Tutin et al. (1964). Casual or weakly naturalized species were those listed in Wagner et al. (1999) that did not meet the criteria for naturalization. These included species recorded from only one or two localized collections and species described using terms that did not clearly indicate naturalization (e.g. "apparently regenerating"). Pest species in Hawai'i were identified based on Motooka et al. (2003) as well as species listed as noxious or having specific negative impacts in Haselwood & Motter (1983). Species introduced to Hawai'i, but not recognized as casuals or naturalized were identified using St. John (1973) and Staples & Herbst (2005). Native species were determined from Wagner et al. (1999).

For Taiwan, presence of introduced species was determined by listing in Yao (1996). Casual and weakly naturalized species were defined as those that were assigned a naturalization status of "rare" or "possibly naturalized" by Wu et al. (2004b). Naturalized species were defined as the remaining species listed as naturalized by Wu et al. (2004b). Pests were defined as the species listed as weeds in Wu et al. (2004a) as well as those rated by Holm et al. (1979) as principle or serious weeds in Taiwan. Native species were identified using Li et al. (1978)

For Fiji, presence of introduced species was determined by listing in Smith (1979–1996), while classifications of casual or weakly naturalized, naturalized, and pest were based on and descriptions given in Smith (1979–1996). Species described using terms such as "occasional escape", "sparingly naturalized" or "adventive" were considered casual or weakly naturalized. Species described as naturalized in general terms were considered naturalized. Pests in Fiji were defined as those described as "weeds" with an adjective indicating the species is abundant or a problem (e.g. "troublesome") or a description of where the weed is a problem (e.g. "abundant weed of sugar cane fields"). Species listed by Holm et al. (1979) as principle or serious weeds of Fiji were also included as pests. Native species were determined using Smith (1979–1996).

For New Caledonia, presence of introduced species was determined using MacKee (1994). Casual and weakly naturalized species were determined from MacKee (1994) based on descriptions such as "spontané" or "parfois naturalisé" with less then three non-cultivated vouchers, while naturalized species were determined as those described as naturalized in general terms or based on non-cultivated vouchers from at least three separate localities. Pest species were determined as those having a weed rating of 2 or 3 for New Caledonia as designated by Swarbrick (1997). These are defined as species whose removal would result in significant increases in yield, or have other useful benefits. Species described by MacKee (1994) as abundant "mauvaises herbes" were also classified as pests, as were species listed as principle or serious weeds by Holm et al. (1979). Native species were determined from Jaffré et al. (2001).

Synonymous species names were identified for each region using the data sources cited above, as well as Missouri Botanical Garden (2006) and Institute of Pacific Islands Forestry (2006). For each island group, four nested species pools were defined based on the sequential and selective process of invasion. The pool of introduced species was defined as species that had been introduced to both island groups in a pair, and had attained at least casual or weakly naturalized status in at least one island group. No attempt was made to identify shared introduced species that had not escaped in any of the island groups, since this double-negative information does not contribute to estimates of the relative invasibility among island groups. The pool of casual and naturalized species was the subset of introduced species that has exhibited at least some capacity to escape; the naturalized species were a subset of the latter pool that met the criteria for naturalization. Because the pest species were defined based on actual and substantial impacts, rather than hypothetical impacts, no casuals or rare escapes were placed the pest category; thus, the pest species were a subset of the naturalized species pool. Because many of the pests were abundant in disturbed anthropogenic habitats, there is a possibility that they could decline or even disappear with changes in human land management, but I have still considered them naturalized because they have attained widespread, abundant and sustained populations.

Results

Across all island groups, 1508 species were recognized as casual or naturalized, and among these, 224 species (15%) were recognized as pests in at least one island group. The remote island group of Hawai‘i has three times as many casual and naturalized species as Taiwan, and this pattern is maintained as the species are filtered into the sequentially smaller pools of naturalized (3-fold greater) and pest species (2.6-fold greater) (Fig. 2). In contrast, the remote island group of Fiji has only 20% more naturalized and casual species than the nearer island group of New Caledonia. This difference diminishes to 1% for the naturalized pool, but then returns to 20% more species in the pest category for Fiji (Fig. 2).

When considering only those species that have been introduced to both island groups in a pair, Hawai‘i still has more casual and naturalized species than Taiwan, but the ratio is reduced from 3.0 to 1.4. This ratio is generally maintained as the species are filtered into the smaller pools of naturalized (1.5) and pest (1.25) species, with no statistical difference in these ratios, as inferred by constancy of proportional representation across statistically independent categories of casuals, naturalized minus pests, and pests ($\chi^2 = 2.2$, $P = 0.32$). The species pool ratios also remain similar when comparisons are made at the level of jointly in-

Table 2. – Species-level congruency, as measured by Jaccard’s Index of similarity between island pairs for nested species pools: casual plus naturalized, naturalized, and pests. Only species that have been introduced to both islands in an island pair are included.

Geographic region	Casual and naturalized	Naturalized	Pests
Hawai‘i vs. Taiwan	0.68	0.64	0.31
Fiji vs. New Caledonia	0.85	0.76	0.40

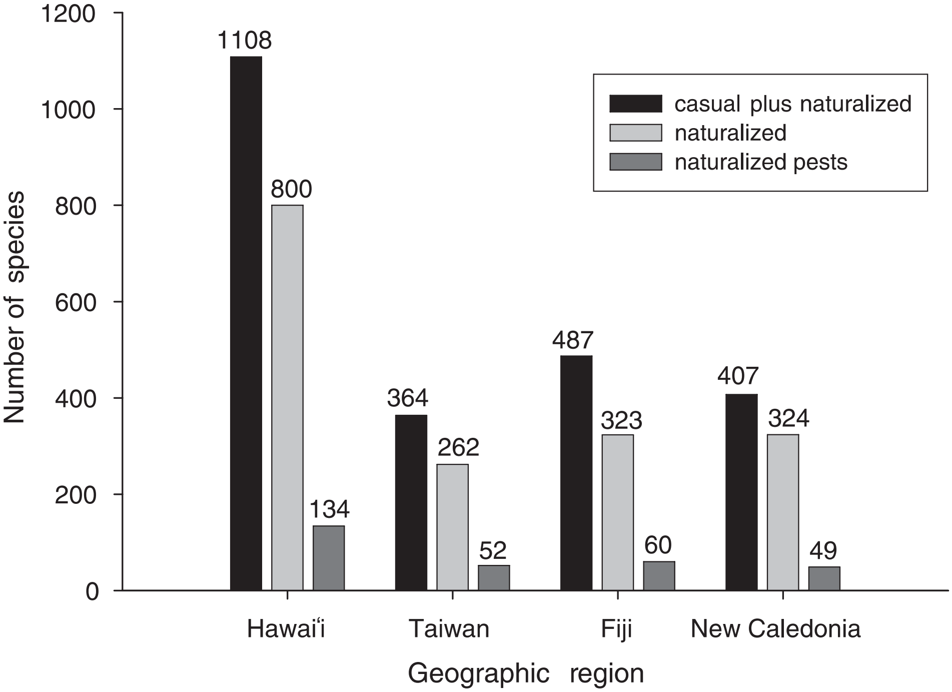

Fig. 2. – Numbers of introduced species reaching different stages in the process of invasion: those that have escaped (casuals plus naturalized), those that have established multiple, sustained populations (naturalized), and those that have become pests (a subset of the naturalized species).

Table 3. – Probability of an introduced species having the same status between paired regions, given that the species was introduced to both regions.

Species status	Paired region	Probability of having the same status within the paired region
Casual and Naturalized in:		
Taiwan	Hawai‘i	0.81
Hawai‘i	Taiwan	0.58
Fiji	New Caledonia	0.81
New Caledonia	Fiji	0.86
Naturalized in:		
Taiwan	Hawai‘i	0.79
Hawai‘i	Taiwan	0.54
Fiji	New Caledonia	0.78
New Caledonia	Fiji	0.73
Naturalized Pest in:		
Taiwan	Hawai‘i	0.34
Hawai‘i	Taiwan	0.28
Fiji	New Caledonia	0.36
New Caledonia	Fiji	0.44

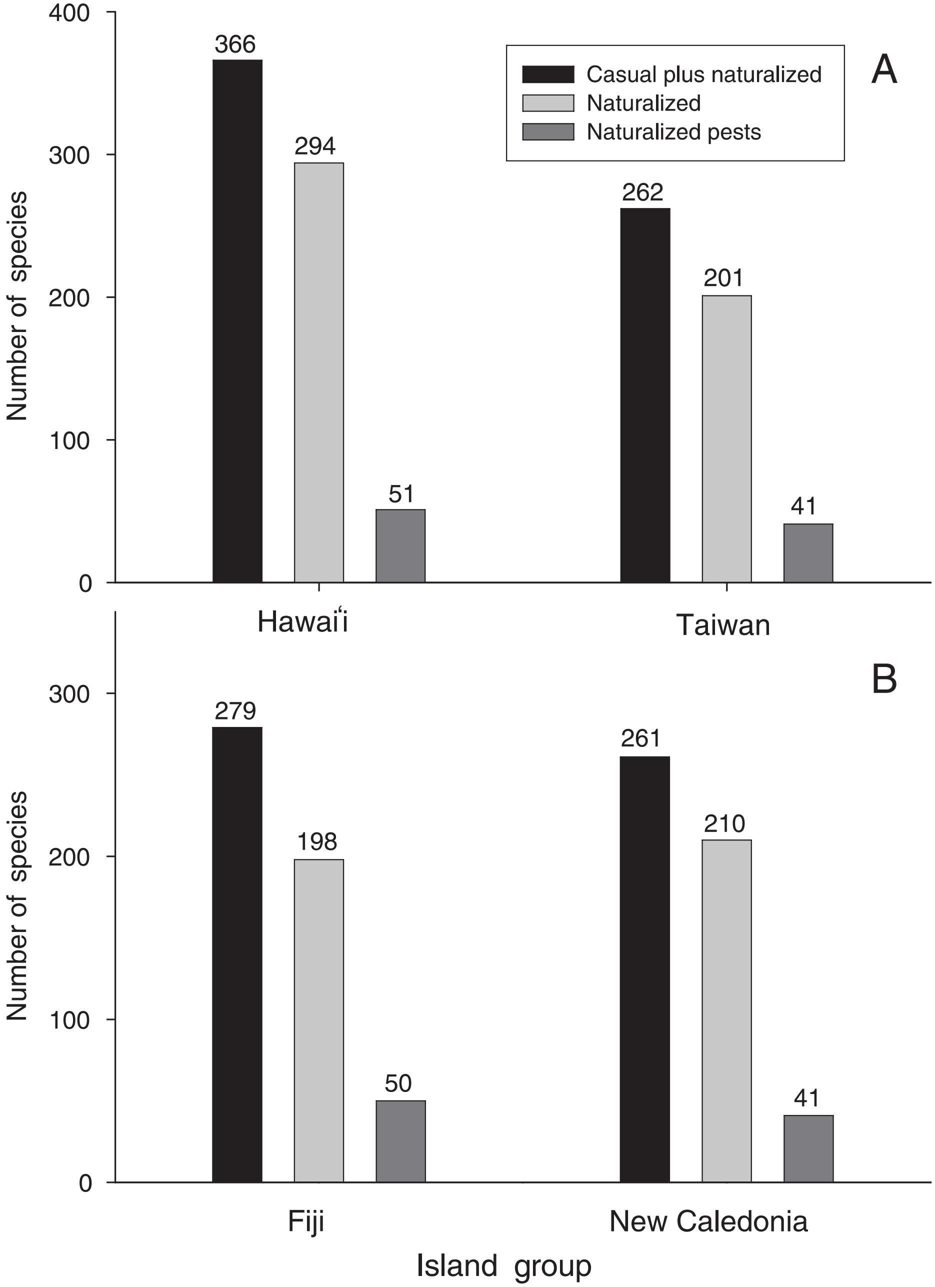

Fig. 3. – Comparison of naturalization categories for island pairs (Hawai'i–Taiwan, A, and Fiji–New Caledonia, B), considering only species that were introduced to both island groups within a pair. See Fig. 2 caption for a description of species categories. Species numbers between island group pairs are not directly comparable because of differing numbers of shared species.

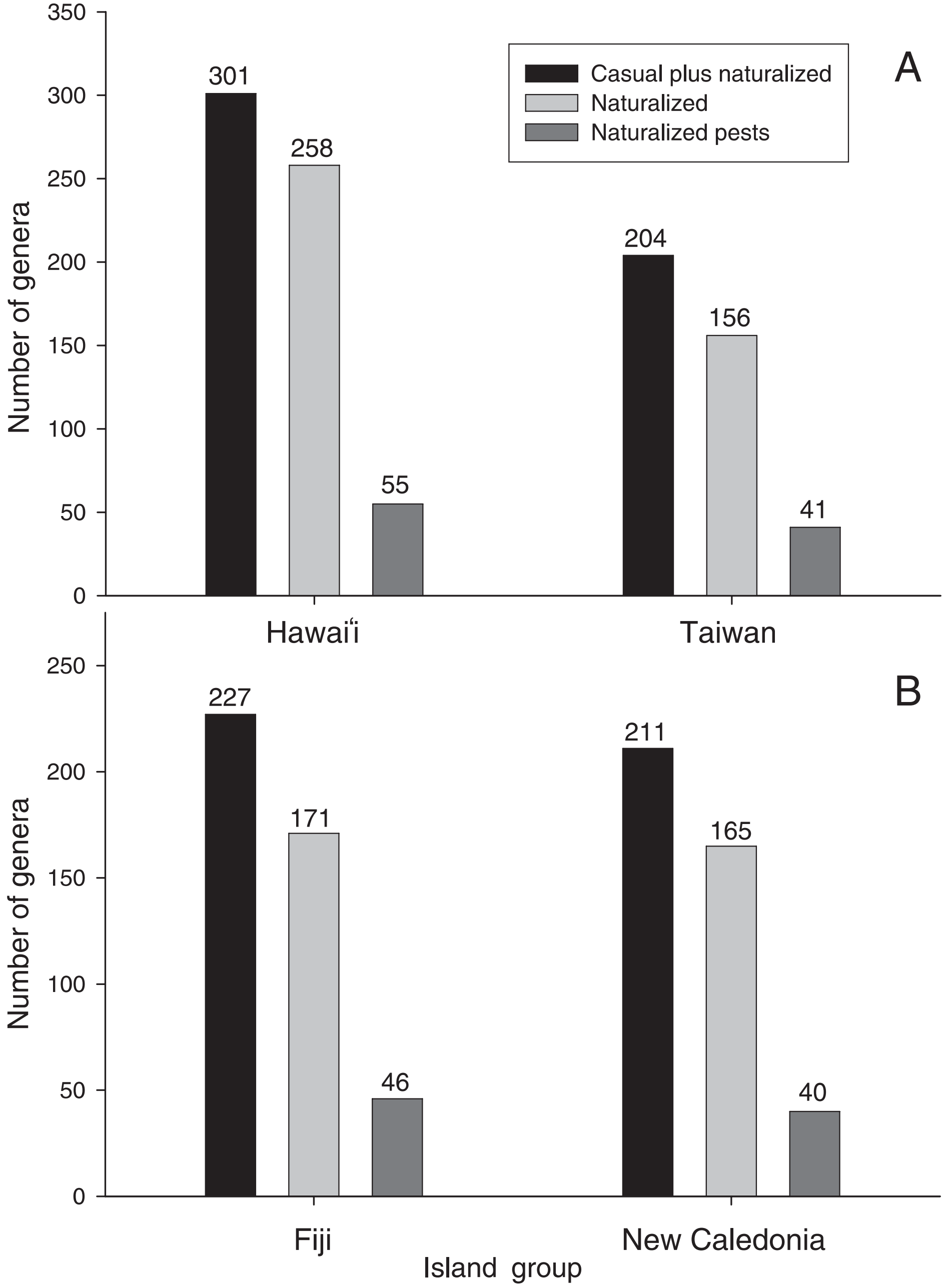

Fig. 4. – Comparison of naturalization categories at the level of genus for island pairs (Hawai'i–Taiwan, A, and Fiji–New Caledonia, B), considering only genera that are known to have been introduced to both island groups within a pair. Numbers of genera between island group pairs are not directly comparable because of differing numbers of shared genera.

troduced genera (Fig. 3). Hawai‘i has more genera at various stages in the invasion process than Taiwan, with ratios of 1.5 (casual and naturalized), 1.65 (naturalized), and 1.3 (pests).

In comparing species that have been introduced to both Fiji and New Caledonia, the more remote island group of Fiji has slightly more casual and naturalized species (ratio 1.07), but in the naturalized pool, the ratio drops to 0.94, and then increases to 1.2 for the pests (Fig. 2). When naturalization status is considered at the level of jointly introduced genera (Fig. 3), the ratios remain similar to the species ratios.

Among those species that were introduced to both island groups within a pair, species congruency was substantially lower in the pest category, as compared with the naturalized or naturalized plus casual pools (Table 2). Furthermore, asymmetries in invasion were apparent between Hawai‘i and Taiwan (Table 3). A species classified as casual or naturalized in Taiwan has an 81% chance of being casual or naturalized in Hawai‘i if introduced, whereas a casual or naturalized species in Hawai‘i has only a 58% chance of attaining the same status in Taiwan (Table 3). In contrast, for Fiji and New Caledonia, the probabilities are symmetrical, at around 80% (Table 3). The probability of a pest in one location becoming a pest in another location, if introduced, ranges from 28% to 44%, depending on the island group where it is a pest.

When rates of naturalization are compared to the number of indigenous (not endemic) species in an island group, there is a significant negative correlation (Fig. 4). Although Taiwan has a ten-fold greater population density than the other island groups (Table 1), and it has presumably experienced greater human disturbance, this appears to be a relatively unimportant factor in determining invasibility, as Taiwan has the lowest rate of naturalization among all the island groups.

Discussion

Propagule pressure

Although tropical islands are often considered highly susceptible to invasion (Simberloff 1995, Denslow 2003), there are clearly differences in susceptibility among tropical islands, as illustrated by the comparison of Hawai‘i and Taiwan. The vulnerability of tropical islands to invasion could be attributable to a combination propagule pressure (a large number of introductions) and higher invasibility relative to mainland areas (Denslow 2003), but no previous study has attempted to partition these two factors. Colautti et al. (2006) suggested that an appropriate null model for invasion biology is that invasibility is determined by propagule pressure. By comparing invasibility before and after filtering out effects of differing numbers of introductions, it appears that roughly half of the three-fold higher number of naturalized plants in Hawai‘i, relative to Taiwan, can be accounted for by higher propagule pressure in Hawai‘i. Differences in the number of human introductions to an area are determined by human behaviours and interest in importing new species. Differences among islands in human yearning for introduced species is rarely emphasized as an explanation for invasibility, perhaps because understanding human behavioural differences lies within the realm of social science, which is unfamiliar to most biologists.

In contrast to differences between Hawai‘i and Taiwan, Fiji and New Caledonia had nearly the same number of naturalized species, irrespective of whether all naturalized species were counted or only shared introductions were counted, suggesting that both propagule pressure (number of introductions) and invasibility, as determined by natural-

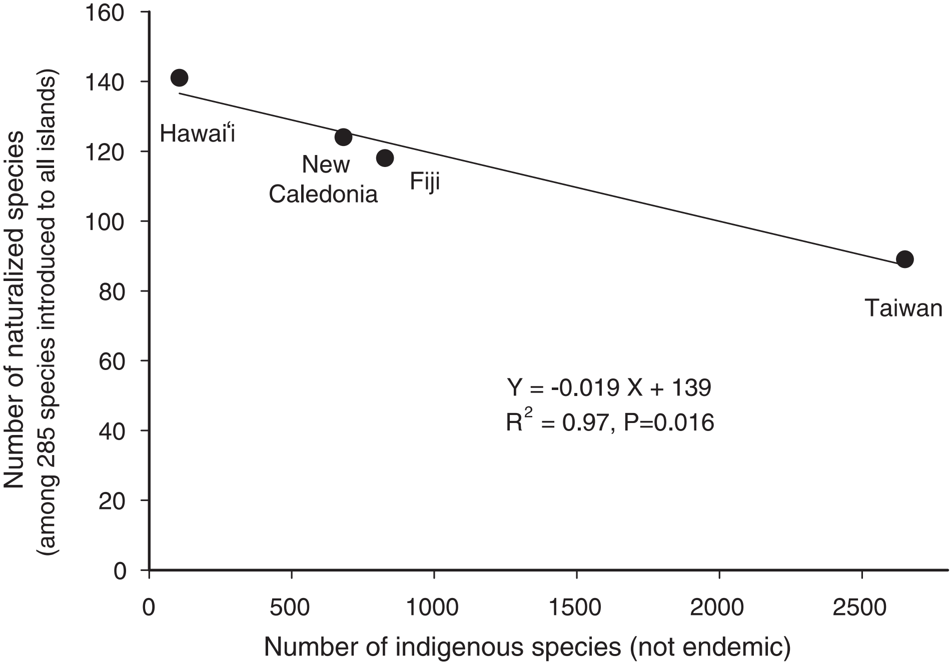

Fig. 5. – Number of naturalized species among a pool of species introduced to all four island groups versus the number of indigenous species in each island.

ization success among shared introductions, is similar between Fiji and New Caledonia. In spite of this, there was some evidence that colonial history (British for Fiji and French for New Caledonia) has influenced the identity of the naturalized species. For example, *Spergularia nicaeensis*, a native of France, is reported from New Caledonia (MacKee 1994) but not from the other island groups.

The present analysis attempted to factor out propagule pressure due to different numbers of unique species introductions between the paired island groups, but another form of propagule pressure is the number of propagules introduced per species (Williamson 1996). I have no reason to expect differences between Hawai‘i and Taiwan in this respect, but to explore this possibility, I tallied the number of non-native species that were classified as naturalized in either Taiwan or Hawai‘i among the non-native ornamental plants listed in Chen (1995). All of these non-native plants are widely planted across Taiwan, and therefore propagule pressure is uniformly high. Fourteen out of the 21 non-native species listed in Chen (1995) were classified as naturalized in Taiwan, whereas 19 out of 21 were naturalized in Hawai‘i, yielding a ratio of 1.4 naturalizations in Hawai‘i per naturalization in Taiwan, despite high propagule pressure in Taiwan. This ratio is almost the same as that for the complete data set of all naturalized species (1.5) and casual plus naturalized species (1.4) known to have been introduced to both island groups, suggesting that numbers of individuals per introduction is not a major factor explaining differences in naturalization between Hawai‘i and Taiwan.

Isolation by distance

Factoring out effects of propagule pressure, Hawai‘i still appears to be more invasible than Taiwan. This pattern matches predictions of the species sampling hypothesis (Herben 2005). The native flora of Taiwan is derived from a larger species pool than that of Hawai‘i (Table 1), so it was expected to be more resistant to invasion. Similarly, the island of Singapore, < 1 km from mainland Asia, appears to be highly resistant to invasion (Teo et al. 2003). Singapore has fewer than 200 naturalized plant species in spite of large numbers of introductions and extremely high levels of human disturbance (Corlett 1988, Teo et al. 2003). Taiwan and Singapore are both islands of continental origin, whereas Hawai‘i is volcanic. Geologic origin might affect invasibility (Teo et al. 2003), but there is no clear mechanism that would explain this. In fact, New Caledonia is continental in origin whereas Fiji is mostly of volcanic origin, yet they are similar in terms of susceptibility to invasion.

By examining numbers and proportions of species that have reached different stages in the invasion process, more insight can be gained regarding the invasibility of Hawai‘i. Hawai‘i does not have a higher proportion of naturalized species or genera that become pests, relative to Taiwan. Rather, the higher invasibility of Hawai‘i begins very early in the invasion process with more escapes (casual and weakly naturalized species), and this difference is propagated through the invasion process, resulting in a higher absolute number of naturalized species and pests in Hawai‘i. In other words, the sequential and selective process of invasion appears to operate in the same way in Hawai‘i and Taiwan, but more species are able to enter the earliest stages of escape in Hawai‘i. This difference is probably not related to greater human disturbance in Hawai‘i, since Taiwan has an order of magnitude higher human population density, and it has experienced similar types of disturbances (deforestation, agriculture, etc). One possibility is that a smaller pool of generalist natural enemies in Hawai‘i imposes fewer barriers on plant reproduction in Hawai‘i, resulting in more escapes (and then more naturalized and pest species), relative to Taiwan. The proportion of naturalized species that became pests in Hawai‘i and Taiwan (15–20%) is comparable to the proportion of naturalized species classified as pests among states in the United States (15–30%), and this supports the suggestion by Rejmánek & Randall (2004) that the number of naturalized species can be a good predictor of the number of pest species.

Fiji was predicted to be more invasible than New Caledonia due to its greater remoteness from a mainland species pool. Although Fiji is more than 1000 km further east in the Pacific than New Caledonia, natural dispersal of plant species to Fiji has been substantial (Table 1), perhaps facilitated by a number of islands that lie in the triangular region connecting Fiji with New Caledonia and New Guinea. These stepping stones, which are largely absent between Hawai‘i and mainland areas, bring Fiji effectively closer to mainland areas, thereby increasing the species pool of natural colonizers and theoretically decreasing its invasibility. In fact, when an isolation index is calculated for Fiji based on the sum of three components: distance to the nearest continent, distance to the nearest similar sized island, and distance to the nearest island group, the isolation index for Viti Levu (a main island of Fiji) is nearly the same as that for New Caledonia (Dahl 1998).

Different indices have been developed to measure island isolation by distance, weighing distances to neighboring islands and continents in different ways (Dahl 1998, Rejmánek & Klinger 2002), but these indices do not account for ocean currents, wind patterns, or pathways used by migratory birds, so indices based solely on physical distances may be inadequate indicators of biological isolation. In contrast, for islands of similar size and habitat diversity, the number of indigenous (non-endemic) species seems to be a better indicator of biological isolation or access to mainland species pools. When the number of indigenous species is used in place of physical distance, both Fiji and New Caledonia fall into place on the line connecting Hawai‘i and Taiwan (Fig. 5), providing support for the species sampling hypothesis of invasibility (Herben 2005). Ideally, for the purpose of testing the species sampling hypothesis, we would want to know the actual number of species that naturally colonized each island group, but this information is not available for most islands. In using the number of indigenous species as a proxy for the number of natural colonists, it is possible that colonizations of more distant islands will be underestimated because colonists of more distant islands may have a greater probability of evolving into endemic species that are not counted. To examine this possibility, I counted the number of genera represented by endemic (but not indigenous) species, added this number to the number of indigenous species. Using this composite index of the number of natural colonists, the slope and coefficient of determination were the same as for Fig. 5 (to two significant digits), indicating that a simple index based on indigenous (not endemic) species may be sufficient for estimating island colonization rates and invasibility.

Congruency of species pools

Among the three nested species pools, pest species were the least congruent within island pairs. This finding was somewhat surprising given that one of the best predictors of an invasive pest is behavior as an invasive pest elsewhere (Reichard & Hamilton 1997, Daehler et al. 2004). Two factors probably contribute to the lower congruence among pest species relative to the other species pools. First, pests are sometimes associated with particular human land uses, and these land uses may vary across island systems. For example, rice, which is widely cultivated in Taiwan, is rarely cultivated in Hawai‘i, so pests that have unwanted impacts only in rice fields might not be classified as pests in Hawai‘i. The second, and probably more important reason for incongruency of pests among island groups, is the added layer of subjectivity in designating pest species (Pheloung et al. 1999). Furthermore, I established an arbitrary threshold of harm to be considered a pest. If the threshold had been lower (thereby including more naturalized species), then congruency would have increased and approached that for naturalized species (up to 80% congruency).

Conclusions

Many accounts of the high susceptibility to invasion of Hawai‘i and other oceanic islands have emphasized the poor competitive ability of native plants and human disturbance (e.g. Pattison et al. 1998, Cox 1999), but high propagule pressure in the Hawaiian Islands appears to account for roughly half of their apparently higher invasibility, relative to Taiwan. The smaller pool of colonizing species that naturally reached the Hawaiian Islands may ultimately be responsible for much of the remaining difference in invasibility between Hawai‘i and Taiwan. The number of indigenous (not endemic) species is probably a better indicator of an island’s biological isolation (access to species pools) than isolation by distance, and it could therefore be a general predictor of susceptibility to invasion, but comparisons need to be made between islands that occur in similar climatic zones with similar habitat diversity. A large number of indigenous plant species does not necessarily provide resistance through direct competition with introduced plants; rather, larger numbers of indigenous plant species are likely correlated with larger numbers and diversity of indigenous representatives of other trophic levels (diseases, herbivores, predators, etc), which as a whole may decrease susceptibility to invasion while also decreasing the overall impacts of introduced species on islands (Simberloff 1995).

Souhrn

Pokud jsou všechny ostatní faktory konstantní, měly by být izolovanější ostrovy náchylnější k invazím, protože jejich původní flóra je odvozena z menšího souboru druhů a mohou na nich chybět důležité funkční skupiny. I když některé analýzy tuto hypotézu podporují, předchozí studie nebraly v úvahu rozdíly v počtu introdukcí rostlinných druhů na jednotlivé ostrovy, které odhady invasibility zkreslují. Stejně tak nebyla v minulosti při hodnocení invasibility brána v úvahu rychlost, jakou jednotlivé druhy naturalizují nebo invadují. Tato práce srovnává stupeň naturalizace zavlečených rostlin na dvou skupinách tichomořských ostrovů, jež jsou ve většině vlastností podobné, liší se však vzdáleností od pevniny. Vliv rozdílů v tlaku propagulí byl eliminován tím, že do srovnání byl zahrnuty jen introdukce společné všem ostrovům. První srovnání ukázalo, že Havajské ostrovy (vzdálené od pevniny 3700 km) mají třikrát více přechodně zavlečených či jen částečně naturalizovaných, plně naturalizovaných a škodlivých invazních druhů než Tchaiwan (vzdálený 160 km od pevniny); pouze zhruba polovina (54 %) tohoto rozdílu je však vysvětlitelná větším počtem introdukcí na Havajské ostrovy. Ve druhé analýze se Fidži (2500 km od pevniny) nelišilo od Nové Kaledonie (1000 km od pevniny) – obě tyto skupiny ostrovů byly vystaveny přibližně stejnému tlaku propagulí a jejich náchylnost vůči invazím je obdobná. Rychlost procesu, během kterého se druh stal invazním, s negativním dopadem na prostředí, je stejná na Havajských i ostatních ostrovech. Vyšší invazibilta Havajských ostrovů vyplývá z vyššího počtu zavlečených druhů, jež jsou v počátečním stádiu invaze (přechodně zavlečené a jen částečně naturalizované); jejich přítomost vede k udržování vyššího počtu druhů naturalizovaných a invazních. Počet původních neendemických druhů byl pro všechny čtyři skupiny ostrovů statisticky průkazně korelován s jejich náchylností k invazi. Pro ostrovy s podobným klimatem a stanovištní diverzitou platí, že počet původních druhů může být lepším prediktorem invazibility než parametry fyzické izolace, protože představuje syntetické měřítko izolace biologické.

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