Invasive Exotic Plants in the Tropical Pacific Islands: Patterns of Diversity

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ABSTRACT

Oceanic islands are good model systems with which to explore factors affecting exotic species diversity. Islands vary in size, topography, substrate type, degree of isolation, native species diversity, history, human population characteristics, and economic development. Moreover, islands are highly vulnerable to exotic species establishment. We used AICc analyses of data on 1132 vascular plant species for 15 countries and 114 islands from the Pacific Island Ecosystems at Risk (PIER) project to examine biological, geographical, and socioeconomic correlates of exotic species richness. PIER provides data on the distribution of naturalized non-native plant species thought to pose environmental or economic risk. We hypothesized that the numbers of PIER-listed species would be positively correlated with island size, habitat diversity, and proximity to major source pools for propagules. Further, we expected numbers of PIER-listed exotic species to be similar among islands in the same country and to be greater where human populations were larger and where economic activity was high. Most species (908) were found on ≤ 10 islands. Species number was significantly correlated with island and country areas and with native plant species richness. The strongest model revealed by AICc analyses of island data included log (area) and maximum elevation as well as country membership, substrate type, and presence of an airport with paved runway (an index of economic activity). By country, AICc analyses revealed two equivalent models, both of which included log (area) and *per capita* gross domestic product as well as a measure of population size (either log (population size) or (population density)). Our analyses provide strong evidence of the roles of biogeographic, environmental, and socioeconomic impacts on the distribution and spread of exotic species.

Key words: biogeography; habitat heterogeneity; Hawaii; PIER; socioeconomic.

THE APPARENT VULNERABILITY OF OCEANIC ISLANDS TO NATURAL-IZATION OF EXOTIC SPECIES IS well known (*e.g.*, D'Antonio & Dudley 1995, Vitousek *et al.* 1997, Sax *et al.* 2002, Kueffer *et al.* 2004, Pyšek & Richardson 2006). Sax *et al.* (2002), for example, estimate that islands have twice as many naturalized exotic plant species as comparably sized patches of mainland landscapes with approximately the same number of native species. A number of factors have been proposed to account for high numbers of non-native plant species on islands, including high habitat diversity, disharmonic floras, low biotic resistance, high resource availability, and mild climates (Loope & Mueller-Dombois 1989, D'Antonio & Dudley 1995, Kitayama & Itoh 1999, Cox & Elmqvist 2000, Denslow 2003). Island communities also may not be particularly resilient to the impacts of exotic species. The impacts of invaders, such as *Miconia calvescens* DC in French Polynesia (Meyer 1994) or exotic grasses in Hawaii (D'Antonio & Vitousek 1992) are commonly cited case studies. Oceanic and some continental islands are characterized by high percentages of endemic species and relatively large numbers of threatened and endangered species (*e.g.*, Brooks *et al.* 2002); small populations put endemic species at risk of extinction under competition from invasive exotics (Meyer & Florence 1996, Loope 1998, Meyer 2000, Myers *et al.* 2000, Brooks *et al.* 2002).

Island nations are also limited in other resources—human, financial, infrastructural, and informational—with which to prevent or manage exotic pests (Sherley 2000).

In many ways islands are good model systems with which to explore patterns of distribution and impacts of invasive plants as well as the efficacy of prevention and control methods (Mack & Lonsdale 2002). Islands vary greatly in size, topography, substrate type, degree of isolation, native species diversity, history, human population characteristics, and economic development. Island ecosystems may provide an intimation of changes to be expected in highly fragmented mainland ecosystems. Impacts of global change including those from sea level rise, altered weather patterns, and increased global trade and travel will be felt severely and early on islands and island economies; all these aspects of global change also are implicated in the spread and impacts of invasive species (Vitousek *et al.* 1997).

In recognition of the need for information on exotic species in the Pacific Islands, the USDA Forest Service, in cooperation with the USGS-Biological Resources Discipline, has compiled an extensive data base on the distribution, identification, biology, and control of invasive exotic plant species on tropical Pacific islands (*Pacific Island Ecosystems at Risk* v. 5.4; Space 2008). Island-specific information on exotic plant species has been compiled from ground surveys, herbarium records, and published information. Here we examine patterns in the diversity of potentially invasive exotic plants from

15 island states in the Central and Western Pacific. We ask whether environmental and biotic correlates of exotic plant species richness among islands are similar to those reported for native plant species and how socioeconomic factors interact with these patterns. We expected the richness of PIER-listed species to be positively correlated with island size (MacArthur & Wilson 1963, Rosenzweig 1995) habitat diversity (Ricklefs & Lovette 1999, Pyšek *et al.* 2002b), and proximity to source pools (Rosenzweig 1995). We used maximum elevation as an index of environmental (habitat) heterogeneity (Mueller-Dombois & Fosberg 1998) and proximity to nearest large pool of propagules as an index of the role of natural dispersal in species occurrences. However, many naturalized non-native plant species have been introduced intentionally for forestry, agricultural, or horticultural purposes (Pickard 1984, Reichard & Hamilton 1997, Daehler & Carino 2000, Mack & Erneberg 2002). We used the presence of an airport with a paved runway to examine the impact of trade on species introductions. Other broad effects of human activity on the spread and impact of exotic species such as through use in reforestation, restoration, gardening, or agricultural activities and through unintentional spread along paths and roadways (Mack *et al.* 2002, Lodge *et al.* 2006) were assessed by testing the association of human population sizes and of economic activity with the numbers of PIER-listed species.

METHODS

Data base overview.—The PIER database has been assembled by J. C. Space and collaborators to provide an authoritative, concise, easily accessible source of information on naturalized exotic vascular plant species (pteridophytes, angiosperms, gymnosperms) on islands in the Pacific Ocean. The data base consists of records of non-native plant species thought to pose environmental or economic risk to Pacific Island ecosystems and includes information on taxonomy, identification, ecology, and control. It is not a list of all naturalized exotic plant species in the islands, but rather a record of the distribution of a set of species thought to be currently or potentially invasive in the islands. For the purposes of this discussion, naturalized species are considered to be those introduced directly or indirectly by humans and found to be reproducing and replacing their populations by sexual or vegetative means without human intervention (*e.g.*, Wagner *et al.* 1999, Pyšek *et al.* 2004). In some cases, such species may become invasive; that is, their populations may reach high densities and they may cause economic or ecological harm (Davis & Thompson 2000, Pyšek *et al.* 2004). It is this group of species documented by the PIER database. We report analyses of PIER Ver. 5.4 (Space 2008).

Species are included in the data base if they are known to be invasive anywhere in their introduced range and if they are known to occur in the focal area whether or not they are invasive on a particular island. They are a subset of all exotic plant species in the islands. Thus, our conclusions address diversity patterns of PIER-listed species, not patterns of all naturalized exotic species. At the time of this analysis (2008), the list of currently or potentially invasive species in the Pacific consisted of 1232 species. New species are

being added continually to the data base as a more complete understanding of their impacts in their introduced ranges is acquired, at which time occurrences on all islands in the data base are updated. Species information compiled from the PIER database is available through the internet (www.hear.org/pier) or on CD by application to the second author.

Records of non-native species.—Distribution records for the PIER list of potentially invasive, non-native species by political unit (countries, territories, and states) and by island were compiled from a combination of sources. Where available, records cited in published literature were used. In addition, we used unpublished agency reports or information surveys compiled by botanists with expertise in the Pacific flora. Of particular importance have been the works of F.R. Fosberg, A.C. Smith, B.C. Stone, W.R. Sykes, W.L. Wagner, W.A. Whistler, and T.G. Yuncker and their collaborators. In some cases, published lists were supplemented by surveys completed between 1998 and 2008 by the second author with assistance from botanists with taxonomic expertise in the flora of the Pacific; these reports are available on line (www.hear.org/pier). Finally, we reviewed collections in the herbarium of the B. P. Bishop Museum, Honolulu, Hawaii. Bibliographic sources for each record can be found in the data base on the internet. Some species, such as *Casuarina equisetifolia* L., are native on some islands and introduced and naturalized or invasive on others. For this analysis, species were recorded only from island groups where we believed them to be introduced.

The complete PIER database contains records from 31 states and 484 islands distributed throughout the temperate and tropical Pacific. In the following analysis, we used information from states and from individual islands when we were confident that we had reasonably recent, complete records of species occurrences. Nevertheless, omissions are likely due to incomplete collections and as-yet-unrecorded introductions. Analyses are restricted to island-states that lie between the Tropics of Cancer and Capricorn in the Central and Western Pacific and for which we could obtain associated biogeographic information. We report information from 15 countries, territories, and states and from 114 islands that met these criteria.

Taxonomy and nomenclature.—We generally follow the nomenclature of the International Plant Names Index (http://www.ipni.org/index.html) and the USDA Agricultural Research Service's GRIN Taxonomy for Plants (http://www.ars-grin.gov/cgi-bin/npgs/html/index.pl?language=en).

Biogeographic information.—Species information was supplemented for the purposes of this analysis by biogeographic information for countries, territories, and states (Table 1) as well as for individual islands where available. We used ArcMap 9.1 (ESRI, Inc. 1995–2007) to calculate island areas and distances to nearest mainland or large-island source pools. Digital copies of island polygons were imported from the U.S. Geological Survey (Hearn *et al.* 2001) and the ESRI (http://arcdata.esri.com/data_downloader/DataDownloader) web sites. Distances to nearest potential sources of exotic species were calculated from the centroids

TABLE 1.   *Countries, territories, and states used in the analysis with biogeographic and socioeconomic information.*

Country	No. islands[a]	PIER species[b]	Native species	Island type[c]	Area[d] (km^2)	Maximum elevation[e](m)	Distance to source[f] (km)	*Per capita* GDP[g](US$)	Population size[h]
Am. Samoa	3	236		v	199	964	2871(NZ)	5800	57,794
Cook Is.	9	401		v/a	240	652	3116(NZ)	5000	21,388
Fiji	34	521	1769	v/a	18270	1324	1968(NZ)	6000	905,949
Guam	1	445	443	v/up	541	406	1821(NG)	15,000	171,019
Kiribati	3	174	66	a	811	81	2814(NG)	800	105,432
Marshall Is	3	285	86	a	181	10	2854(NG)	2300	60,422
Federated States of Micronesia	6	383		v	702	791	1658(NG)	3900	108,004
Nauru	1	215	50	up	21	61	2080(NG)	5000	13,287
New Caledonia	15	600	3332	c/a/up	19,060	1628	1480(AU)	yes	219,246
Niue	1	307	175	up	260	68	2434(NZ)	yes	2,166
Northern Mariana Islands	14	298	420	v/up	477	965	2096(NG)	yes	82,459
Palau	9	344		v/up	458	242	879(PH)	no	20,579
Samoa	2	321		v	2944	1857	2816(NZ)	yes	176,908
Tonga	4	351	450	up	748	1033	2053(NZ)	yes	114,689
Hawaiian Islands (US)	8	892	956	v	16,637	4205	3846(NA)	no	1,275,194

[a]Number of islands used in the analysis; [b]Number of PIER-listed species recorded as introduced to this country; [c]Island type: a = atoll, up = uplifted atoll, c = continental, v = volcanic; atolls and uplifted atolls have coralline substrates. Some islands have more than one origin. [d]Total area of all islands in the group; [e]Maximum elevation in the island group; [f]Distance to nearest large source pool of species, AU = Australia, PH = Philippines, NG = New Guinea, NA = North America, NZ = New Zealand; [g]*Per capita* gross domestic product. Data from 2000–2005 (Central Intelligence Agency 2006); [h]Population size in 2006 (Central Intelligence Agency 2006).

of the island states. Socioeconomic information, such as population sizes and *per capita* gross domestic product (PCGDP), were obtained from *The World Factbook* published on the web by the U.S. Central Intelligence Agency (https://www.cia.gov/cia/publications/factbook). A variety of published atlases, country reports, and online sources were consulted for information on the distribution of airports with paved runways, substrate composition, maximum elevation, and colonial history.

STATISTICAL APPROACH.—Data were sorted and subsetted in Paradox Ver. 11.0 (Corel Corporation, 1996–2003). We explored several hypotheses regarding factors likely to affect the diversity of invasive species on individual islands. These hypotheses informed the choice of regression models compared using AICc analysis for small sample sizes (Burnham & Anderson 2002). Because species richness is widely demonstrated to be a positive function of the area (Rosenzweig 1995), we assumed that numbers of PIER-listed species would be a significant positive function of island area. Thus we included log (area) as an independent variable in all models and asked whether habitat heterogeneity and/or isolation improved the prediction of PIER-listed species. We expected more PIER-listed species where habitat heterogeneity was high (*e.g.*, Rosenzweig 1995), in this case as indexed by maximum elevation, and fewer species on isolated islands in comparison to those close to potential source pools. Where data on maximum elevation were missing, we replaced the missing datum with the median value for that island type (volcanic island, atoll, uplifted atoll, or continental island) within that country/state.

Several other factors also may affect these relationships. Islands within political units with a shared history of colonization and immigration, social structure, culture, and agricultural development are likely to be more similar to each other than to islands in different political units. Thus, we expected political unit membership to be an important predictor of number of PIER-listed species on islands. Islands in the data base included those with coralline substrates such as atolls and uplifted limestone islands as well as those with volcanic, metamorphic, and/or ultrabasic soils as on some continental and volcanic islands. Some islands had diverse substrates. We hypothesized that islands with coralline substrates would be less species-rich than islands with other substrate types because of the limitations to plant growth that often characterize coralline islands (*e.g.*, excessive drainage, high salinity, coarse substrate, thin calcareous soils, Mueller-Dombois & Fosberg 1998). We hypothesized that islands characterized by significant international commercial activity would have more PIER-listed species than islands dominated largely by local commerce because such activity would promote transport in exotic species, repeated introductions, and disturbance. We indexed the difference in commercial activity by the presence or absence of airports with paved runways able to support jet airplanes.

Using the island data base, we compared performances of seven linear regression models in PROC MIXED (SAS Institute, Inc. 2003) on the basis of Akaike's Information Criterion for small samples (AICc) (Burnham & Anderson 2001, 2002). AICc is a function of the residual mean square error, sample size, and the number of variables in the equation. An AICc analysis seeks to assess the relative goodness of different models and is particularly

useful where variables are likely to be interdependent. The model for which AICc is smallest is seen to be the best model from among those included. Relative goodness of the models is assessed on the basis of ΔAICc (the difference in AICc from the best model) and of AICc weight, a measure of how well one model is supported relative to all other models (Burnham & Anderson 2002). In general, models in which ΔAICc > 10 are not supported. Because AICc analysis evaluates only the relative performance of the best of several models, we also examined the goodness of that model, the fixed effects of selected individual variables and contrasts of interest using PROC GLM (SAS Institute, Inc. 2003).

We further examined differences among countries in the total number of PIER-listed species among all islands in the unit using AICc comparisons of models including log (total island area), *per capita* gross domestic product (PCGDP), population density, log (population size), and maximum elevation. As with the island-based analysis, we assumed that total area (as log [area]) would be positively correlated with number of PIER-listed species. Thus all models included log (area) as a variable. We hypothesized that habitat heterogeneity as indexed by maximum elevation and high levels of human activity as measured by population size, population density, and PCGDP would be positively correlated with numbers of PIER-listed species.

RESULTS

We summarized data on the distribution of 1132 PIER-listed species in 15 countries, territories, or states and 114 islands. Species were distributed among 142 families, the most species-rich of which were Poaceae (188 species), Fabaceae (135 species), and Asteraceae (88 species). Frequency distributions of species among 114 focal islands are given in Fig. 1. As with many native floras, most exotic species were rare; 148 PIER-listed species were found on only one island and 760 were found on ten or fewer islands. The ten most widely distributed exotic species occurred on 51–65 islands; they included five grasses (*Eleusine indica* [L.] Gaertn.*, Cenchrus echinatus* L.*, Paspalum conjugatum* P. J. Bergius), *Cynodon dactylon* (L.) Pers., and *Chrysopogon aciculatus* (Retz.) Trin., three herbs (*Stachytarpheta cayennensis* [Rich.] Vahl*, Ageratum conyzoides* L.*,* and *Chamaesyce hirta* [L.] Millsp.) and three trees (*Leucaena leucocephala* [Lam.] de Wit, *Psidium guajava* L. *C. equisetifolia* L.) Herbs were the most common growth forms (431 species), followed by grass-like forms (213 species), trees (197 species), and shrubs (172 species). Vines (92 species), aquatic herbs (25 species), succulents and bromeliads (17 species), and ferns (seven species) made up the balance.

The islands included in the data set are characterized by a wide variety of environmental and socioeconomic attributes (Table 1). Volcanic islands are the most common (50.9%), followed by atolls (19.3%), uplifted coralline islands (15.8%), and continental islands (9.6%). Volcanic islands are characterized by higher relief (median maximum elevation 533 m asl) and larger areas (3445 ha) than continental islands (66 m asl, 2202 ha) atolls (5 m asl, 1117 ha) and uplifted coralline islands (65 m asl, 2195 ha). Islands in the data base

included those with coralline substrates such as atolls and uplifted limestone islands, with basaltic substrates on volcanic islands and with metamorphic and ultrabasic substrates as on some continental islands. The largest islands are Grande Terre (New Caledonia, continental, 1,756,574 ha), Hawaii Island (United States, volcanic, 1,105,802 ha), and Viti Levu (Fiji, volcanic, 1,096,303 ha), whereas the smallest islands are Fanna (Palau, uplifted coralline, 36 ha), Rotumba (Fiji, volcanic, 57 ha), and Katafanga (Fiji, atoll, 89 ha). All are relatively distant from their nearest major sources of plant propagules, but the Hawaiian Islands (4131–4464 km from North America) are considerably more isolated than the islands of Palau (395–903 km from New Guinea), which are the closest to major potential seed sources. About a third of the islands lie in areas characterized by low typhoon frequency (Pacific Islands Applied Geoscience Commission 2006).

Early human colonization of the islands occurred between 1100 BC and AD 750 by Melanesians (three countries), Micronesians (six countries), and Polynesians (six countries) (Juvik & Juvik 1998). Many islands have been occupied subsequently by one or more other countries in the last 300 yr, including Australia, Britain, France, Germany, Japan, New Zealand, Spain, and the United States. Today, widely divergent socioeconomic conditions in the islands of Oceania are illustrated by the range of population densities (Niue: 0.08 people/ha; Nauru: 7.27 people/ha) and *per capita* gross domestic product (PCGDP) (Kiribati: $800; Hawai'i (US): $39,871).

Numbers of PIER-listed species by island were significantly correlated with island area ($z = 0.54$), as well as maximum elevation and distance to potential propagule sources (Table 2; Fig. 2). Correlation analysis of PIER-listed species richness by country-state revealed significant associations with total island area and maximum elevation as well as with population size, population density and percent GDP (Table 2). Biogeographic characteristics were not mutually independent. For example, island area also was correlated
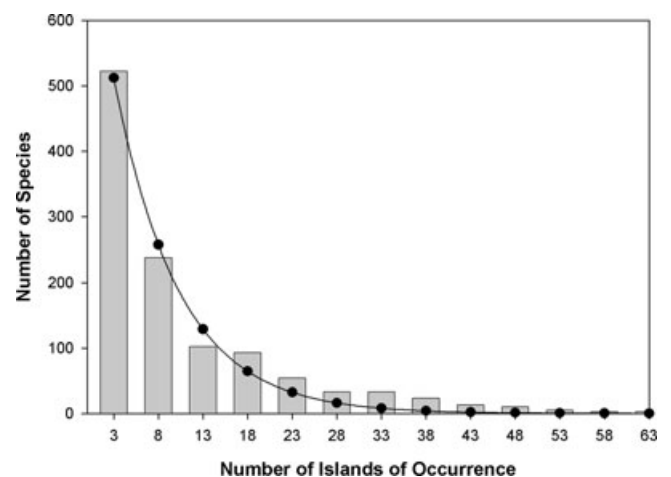

FIGURE 1.   Frequency distribution of island occurrences of PIER-listed species (bars). Dots track expected distribution based on a negative exponential decay function.

TABLE 2.   *Pearson correlation coefficients r between number of PIER-listed species and island or country attributes.*

Parameter	Islands	P	Countries	P
Biogeographic				
Log (area)	**0.740**	< 0.0001	**0.756**	0.001
Maximum elevation	**0.669**	< 0.0001	**0.841**	< 0.0001
Distance to source	**0.428**	< 0.0001		
Socioeconomic				
Per capita GDP			**0.864**	< 0.0001
Population size			**0.834**	0.0001
Population density			−0.406	0.136

Coefficients in bold are significant following application of Bonferroni's correction for multiple comparisons.

FIGURE 3.   Native versus PIER-listed invasive exotic species in 11 island countries for which we had reliable data on both indigenous and exotic species. Regression equation: PIER-listed Species = 260.9 + 0.10 (native species); $N = 11$, $P = 0.030$, $R^2 = 0.42$.

significantly with maximum elevation ($r = 0.630$, $P < 0.0001$, $N = 114$) and with distance to propagule source ($r = 0.290$, $P = 0.0018$, $N = 114$). Numbers of PIER-listed species and native species richness were correlated for 11 island states for which data on native species were available ($r = 0.632$, $v = 9$, $P < 0.05$; Fig. 3). The State of Hawaii with 892 PIER-listed species to 1168 species of indigenous vascular plants was an outlier.

AICc ANALYSIS.—.Numbers of PIER-listed species ranged between one and 656 with a mean of 104.9 species for 114 islands. AICc analysis of island data found the strongest model (AICc weight = 0.902; Table S1) to include log (area) and elevation as well as three class variables (country, substrate, and airport). The next best model included all of these variables plus distance from nearest major propagule source. However, this model was less well supported than
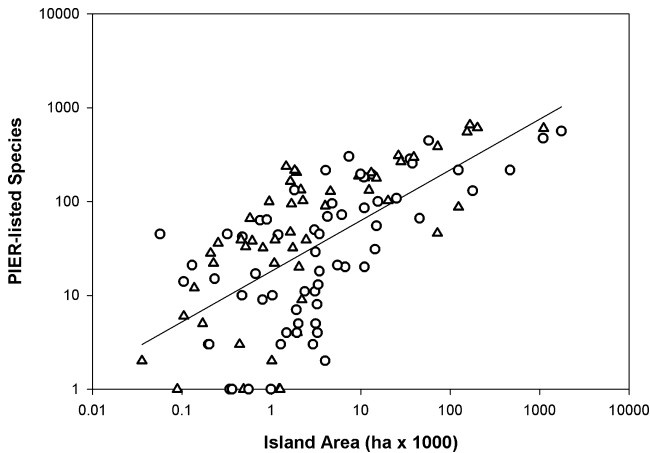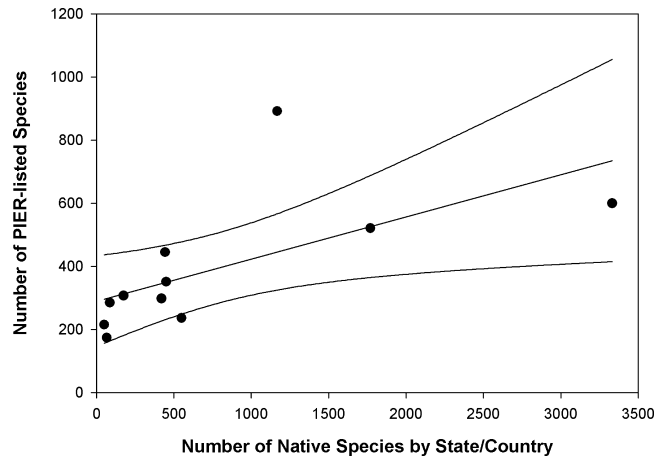

FIGURE 2.   Species-area curve for numbers of PIER-listed species on oceanic islands. Circles represent islands with predominantly volcanic or metamorphic substrates. Triangles represent islands with predominantly coralline or limestone substrates.

the best model (ΔAICc = 4.448; AICc weight = 0.098). Goodness-of-fit statistics suggest that the model is robust. The assumption of normality was not violated in the distribution of the data nor of the residuals. Estimated standard error of the mean as predicted by the best model was small (SE = 5.6) and R^2 was 0.859. Type III tests of fixed effects revealed significant positive slopes of the regression of PIER species on log (area) ($F = 12.18$, $P < 0.0001$) and elevation ($F = 29.74$, $P < 0.0001$). Class variables country ($F = 5.09$, $P < 0.0001$) and airport ($F = 30.30$, $P < 0.0001$), but not coralline substrate ($F = 1.51$, ns), significantly affected the intercept. On average, presence of an airport with a paved runway added 108 PIER-listed species ($\pm$ 19.7 SE, $t = 5.50$, $P < 0.0001$). The Hawaiian islands had on average 76.5 ($\pm$ 28.7, $t = 2.66$, $P = 0.009$) more species than other islands, but New Caledonian and Fijian islands had on average 78.5 ($\pm$ 18.5, $t = -4.23$, $P < 0.0001$) and 55.0 ($\pm$ 15.7, $t = -3.50$, $P = 0.0007$) fewer species, respectively.

By country, numbers of PIER-listed species varied between 174 (Kiribati) and 892 (State of Hawaii) with a mean of 384.9 $\pm$ 46.4 SE AICc analysis revealed two equivalent models (Table S2; ΔAICc = 0.612). In addition to log (area) both included PCGDP and a measure of population size (log [population] or population density). Two other models had somewhat larger ΔAICc values, indicating that they were less well supported; in addition to log (area), the two included maximum elevation in addition to population size or density as a parameter but did not include PCGDP. Type III tests of fixed effects for the best model showed significant effects for log (area) ($F = 8.08$, $P < 0.0160$) and for PCGDP ($F = 26.45$, $P = 0.0003$) but not for log (population) ($F = 0.40$, ns). This model explained 87.6 percent of the variation in PIER-listed species among countries with an SE of the mean of 18.4.

DISCUSSION

Analysis of the distributions of PIER-listed exotic species reveals patterns consistent with previous island biogeographic studies, namely, the strong correlations between species richness and island area and between native and exotic species richness (*e.g.*, Lonsdale 1999, Sax & Gaines 2003, Jarnevich *et al.* 2006). Well-established theory predicts higher species diversity on large than small islands because populations are likely to be larger on large islands and thus less prone to extinction than on small islands (MacArthur & Wilson 1963, Magurran 1988, Rosenzweig 1995). Large islands also are likely to have a greater diversity of habitats than small islands. Like island area, habitat diversity is commonly shown to be positively correlated with species diversity (Johnson & Raven 1973, Ricklefs & Lovette 1999, Pyšek *et al.* 2002b, Price 2004, Jarnevich *et al.* 2006). Islands with high topographic relief exhibit a wider range of temperature and rainfall, than those of low relief (*e.g.*, Mueller-Dombois & Fosberg 1998) and are also likely to support a greater range of freshwater habitats than low islands (Haynes 1990). The high islands of Hawaii, for example, are characterized by rainfall rates that range from 0.3 to 15 times that of rainfall in the adjacent open ocean (Loope 1998) and by life zones from subtropical desert scrub and rain forest to subtropical alpine rain forest (Tosi *et al.* 2002). In this study, both island area and maximum elevation were included in the best model as determined by the AICc analysis and both yielded significant fixed effects.

The high z-value for the species-area curve of PIER-listed species ($z = 0.54$), somewhat above that commonly reported for true islands ($z = 0.25$–0.33; Rosenzweig 1995), suggests that the island area effect is particularly strong for invasive plants. Large, habitat-diverse islands may support not only more species of habitat specialists, but also more habitat generalists whose persistence is enhanced by the availability of multiple suitable habitats on large heterogeneous islands (Ricklefs & Lovette 1999, Mack 2000). Human-mediated introductions of exotic species will be more frequent and more varied on large islands with substantial human populations and economic activity. Large islands may enhance population 'rescue' effects (Ricklefs & Cox 1972); introductions to different habitats, at different seasons and under different circumstances may rescue failing populations and reduce extinction rates. Numbers of PIER-listed species were positively correlated with human population density, *per capita* GDP, and the presence of airports, all of which also were correlated with island or country area. Grasses and forbs were the most widespread growth forms in the islands as they are among other floras of naturalized exotic plants (*e.g.*, plants introduced between North America and Eastern Asia; Ricklefs *et al.* 2008).

Native species diversity was a good predictor for numbers of PIER-listed species as it has been for numbers of non-native species in other studies (*e.g.*, Levine & D'Antonio 1999, Lonsdale 1999, Stohlgren *et al.* 1999, Levine 2000, Richardson *et al.* 2005). Previous authors have interpreted this correlation as evidence that the two groups respond similarly to environmental factors such as productivity, nutrient supply, and habitat diversity (Hooper *et al.* 2005, Chabrerie *et al.* 2008), which often are correlated with high species diversity (*e.g.*, Currie & Paquin 1987, Jarnevich *et al.* 2006). In the case of the Pacific islands, we were not able to examine effects of factors other than area on native species richness. In the case of exotic species, history and socioeconomic patterns also play a strong role as shown by the inclusion of country identity in the best island model. For example, the Hawaii archipelago has almost 80 more species per island than other Pacific islands and more species (892) than might be expected (445) from the number of native vascular plants recorded. The unusually high numbers of PIER-listed species in Hawaii may be attributed in part to its historic role as a hub of Pacific trading routes and also to extensive reforestation efforts during the 20th century. Between 1910 and 1960, 1026 species of vascular plants, all exotic except for 78 native species, were out-planted into forest reserves statewide (Woodcock 2003). While the objective was to restore Hawaii's watersheds, the project also provided opportunity for the establishment and spread of invasive exotic species into native forests at an unprecedented scale. Historic afforestation projects have contributed also to the exotic flora of Australia (Lonsdale 1994), but not apparently to that of Hong Kong (Corlett 1999) or Puerto Rico (Thompson *et al.* 2007) where assessments found that few exotic species used for reforestation or plantations in the past had naturalized or posed a threat to native forest.

At a local scale, studies of parks have shown that exotic species diversity reflects the presence of human settlements and gardens (Sullivan *et al.* 2005), human visitation rates to parks (Lonsdale 1999), and human population sizes (Pyšek *et al.* 2002a, Jarnevich *et al.* 2006). Many invasive exotic plants were introduced for gardens and horticultural, pasture, or forestry enterprises (Lonsdale 1994, Reichard & White 2001, Mack & Erneberg 2002). For example, 74 percent of environmental weeds in New Zealand originated as garden plants (Buddenhagen *et al.* 1998) and most of the worst environmental weeds in Hawaii were originally horticultural introductions (Daehler & Carino 1999). In today's global economic environment, movement of plants even to remote oceanic islands is easily accomplished. High levels of economic activity suggested by the presence of jet airports or high *per capita* GDP is likely to be correlated with personal and business travel, horticultural and agricultural development, and import markets, all of which may facilitate introduction of exotic plants.

Ecosystem disturbances also facilitate the establishment and spread of non-native species (Mack *et al.* 2002). Islands are subject not only to the full range of anthropogenic disturbances, but also may be chronically struck by typhoons and hurricanes. In Jamaica, Bellingham *et al.* (2005) found that hurricanes facilitated the spread of the exotic shrub *Pittosporum undulatum* Ventenat in native forests. Similar typhoon effects have been seen in Tahiti (Meyer 1994) and Florida (Horvitz *et al.* 1998). However, other reviews have found that vegetation on some islands subject to frequent typhoons may regenerate rapidly following wind disturbances with little change in species composition (Brokaw & Walker 1991, Franklin *et al.* 2004, Thompson *et al.* 2007). Our data were not adequate for evaluating the role of typhoon frequency on island ecosystems. Consequences of altered typhoon frequencies and strengths associated with climate change can be expected to affect

forest structure and composition in as yet little understood ways in the Pacific Islands.

IMPACTS OF EXOTIC PLANTS ON ISLAND ECOSYSTEMS.—The literature provides a lively discussion of the impacts of exotic plants on island ecosystems. On the one hand, they are widely seen as a threat to endangered species and thus to the native plant diversity of tropical islands. Polynesia/Micronesia was listed by Myers *et al.* (2000) and by Hobohm (2003) as a biodiversity hotspot because of the high numbers of endemic species and small habitat areas. Brooks *et al.* (2002) suggested that the vulnerability of oceanic islands to habitat loss likely is underestimated because of the added impacts of exotics on the native flora and fauna. Similarly, Meyer and Florence (1996) emphasized the danger posed by the invasive *M. calvescens* DC to Tahiti's endemic flora and Cox and Elmqvist (2000) note that alien species threaten 90 percent of Hawai'i's endemic plants.

In contrast Davis (2003) and Gurevitch and Padilla (2004) argue that evidence of competition from invaders is equivocal and not likely to be the prime cause of species extinctions; rather habitat loss and intertrophic interactions, such as rat depredation (Athens 1997, Hunt 2006) are seen to have considerably stronger impacts. Moreover, exotic plants in secondary forests, plantations, and managed forests may facilitate site rehabilitation and the establishment of native species (Ewel & Putz 2004, Lugo 2004). Sax and collaborators observed that the spread of exotic plants has approximately doubled the floras of oceanic islands with no concomitant loss of indigenous species (Sax *et al.* 2002, Sax & Gaines 2003). Island biogeographic theory predicts that an increase in effective dispersal rates, such as that observed with the global transport of plants, should result in a shift in the equilibrium number of species toward higher species richness; there is no basis, in island-biogeographic theory at least, to hypothesize a local loss in indigenous species as a result of exotic species establishments, although there may eventually be a global decline in diversity (Rosenzweig 2001). Finally, exotic species may be a reflection rather than the cause of ecosystem degradation (MacDougall & Turkington 2005). In addition to competitive effects, however, exotic species may alter ecosystem processes such as nutrient supply (Vitousek *et al.* 1987, Hughes & Denslow 2005, but see Kueffer *et al.* 2008) and fire frequency (D'Antonio & Vitousek 1992) and may reduce productivity of the land for crops and livestock (Mack *et al.* 2002). Invasions that alter ecosystem processes may have more substantial impacts on native species than those having competitive impacts alone.

Management of current and potentially invasive exotic species should remain a high priority for island countries (Sherley 2000). Scarce suitable native species for watershed rehabilitation, agriculture, forestry, and horticulture provide a strong incentive to use exotic species to meet local needs, although long-term impacts can be severe. Clearly, species used in restoration efforts should be selected with care and those that have shown evidence of causing ecological or economic damage elsewhere should be avoided (Ewel *et al.* 1999). The positive correlation between native and exotic species diversity suggests not only that areas and habitats rich in native species may be especially vulnerable (Jarnevich *et al.* 2006), but also that productivity and disturbance, which affect native diversity, might also

be manipulated to manage invasive species (Huston 2004, Denslow 2007). Among the Pacific islands, high priority sites for monitoring should be islands of high relief (high habitat diversity) and moist to wet habitats, both of which exhibit high native and non-native species diversity (Price 2004). The emergence of factors such as presence of an airport able to take large planes, human population size, and *per capita* GDP all emphasize the vulnerability of islands with high economic activity to invasive species introductions. Scarce resources for biodiversity conservation and invasive species control might go farther when invested in outer islands were human impacts may be less. Finally, regional cooperation to develop information, infrastructure, and expertise to address invasive species issues can help leverage scarce resources and focus action where it is likely to be most effective.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *AICc comparison of models predicting numbers of PIER-listed species on 114 tropical Pacific islands.*
TABLE S2. *AICc analysis of models explaining the number of PIER-listed species in 15 Pacific Island countries or states.*

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