

## Species richness and patterns of invasion in plants, birds, and fishes in the United States\*

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### Abstract

We quantified broad-scale patterns of species richness and species density (mean # species/km<sup>2</sup>) for native and non-indigenous plants, birds, and fishes in the continental USA and Hawaii. We hypothesized that the species density of native and non-indigenous taxa would generally decrease in northern latitudes and higher elevations following declines in potential evapotranspiration, mean temperature, and precipitation. County data on plants ( $n = 3004$  counties) and birds ( $n = 3074$  counties), and drainage (6 HUC) data on fishes ( $n = 328$  drainages) showed that the densities of native and non-indigenous species were strongly positively correlated for plant species ( $r = 0.86$ ,  $P < 0.0001$ ), bird species ( $r = 0.93$ ,  $P < 0.0001$ ), and fish species ( $r = 0.41$ ,  $P < 0.0001$ ). Multiple regression models showed that the densities of native plant and bird species could be strongly predicted (adj.  $R^2 = 0.66$  in both models) at county levels, but fish species densities were less predictable at drainage levels (adj.  $R^2 = 0.31$ ,  $P < 0.0001$ ). Similarly, non-indigenous plant and bird species densities were strongly predictable (adj.  $R^2 = 0.84$  and  $0.91$  respectively), but non-indigenous fish species density was less predictable (adj.  $R^2 = 0.38$ ). County level hotspots of native and non-indigenous plants, birds, and fishes were located in low elevation areas close to the coast with high precipitation and productivity (vegetation carbon). We show that (1) native species richness can be moderately well predicted with abiotic factors; (2) human populations have tended to settle in areas rich in native species; and (3) the richness and density of non-indigenous plant, bird, and fish species can be accurately predicted from biotic and abiotic factors largely because they are positively correlated to native species densities. We conclude that while humans facilitate the initial establishment, invasions of non-indigenous species, the spread and subsequent distributions of non-indigenous species may be controlled largely by environmental factors.

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## Introduction

Harmful plants, animals, and diseases in the United States may be the most challenging environmental threat of the 21st century. It is estimated that more than 6500 species have been introduced in the USA since European settlement (Williams and Meffe 1998), with economic costs estimated to be greater than \$137 billion/year (Pimentel et al. 1999). Local patterns of invasions have been well documented for a few species or biological groups in various areas such as introduced birds in Hawaii (Moulton et al. 2001), aquatic invaders in the San Francisco Bay (Cohen and Carlton 1995), or the brown tree-snake in Guam (Fritts and Rodda 1995). Still, little is known about the general patterns of species introductions for multiple biological groups at state-wide or national scales. Despite incomplete data, we must begin to document the broad-scale patterns of invasion of multiple biological groups to set priorities for prevention, early detection, containment, and restoration.

General ecological theories that attempt to explain the patterns of biological diversity may guide such inquiry. Currie (1991) summarized alternative explanations for the well-known latitudinal gradient in species diversity and found that declining richness of trees, birds, mammals, amphibians, and reptiles as one moves from the equator to the poles was best explained by declines in evapotranspiration and solar radiation. This pattern of association suggests that diversity peaks at those places with optimal conditions for growth and productivity (Currie 1991; Rosenzweig 1992; Huston 1979, 1994; Badgley and Fox 2000; Hawkins et al. 2003; what Ricklefs 2004 called 'local determinism').

In addition, species richness of one taxon may propagate through the food web, particularly if there are strong coevolutionary interactions. It follows that the richness of plant pollinators may track plant species richness. Indeed, the richness of carnivore species increased with the number of herbivore species, and the number of predator species increased with the number of victim species (Rosenzweig 1995). Local determinism gives us hope for predicting native species richness from a few easily measured environmental factors (Palmer 1994; Mack 2002).

Still, patterns of diversity may be difficult to predict at large spatial scales. We owe much to Ricklefs' (2004) more complex framework for global patterns of biodiversity, where he clarifies that contributions to local and regional diversity are a hybrid of environmental conditions and constraints, regional processes and historical events (in an evolutionary context), and changing population dynamics and niche widths with changes in species richness. He challenges ecologists to, among other things, 'raise regional and historical factors to equal footing with local determinism in their influence on the diversity environment relationship and geographical patterns of diversity in general' (Ricklefs 2004, p. 1).

Today's ecologists are further challenged to reconcile the historical patterns of long-evolved native species with the emerging and rapidly evolving patterns of recently arrived non-indigenous species. Based on local determinism, it logically follows that the different native and non-indigenous biological groups might track each other in richness patterns, assuming they respond to each other and to similar energy and resource limitations in the broadest sense. However, if history, evolution, and adaptation have filled available niches to capacity with native species, there might be few niches available for similarly-adapted newcomers. Thus, successful invasion may be conditioned on some sort of disturbance to open the system to colonization by non-indigenous species (Rejmánek 1989; D'Antonio et al. 1999).

Some studies have found evidence that the richness of native and non-indigenous species covary positively – a pattern observed at multiple spatial scales. At the scale of 0.1 ha plots in the Central Grasslands, Rocky Mountains of Colorado, and arid ecosystems in southern Utah, Stohlgren et al. (1997, 1999a, 2002) observed significant positive relationships between native and non-indigenous plant species richness (and density, in 0.1-ha plots). Furthermore, there were many cases where native and non-indigenous species richness was positively correlated to soil fertility, light, and water availability. At continental scales, preliminary county-level data showed that native plant species were positively correlated to non-indigenous species richness in 45 of the 46 states (Stohlgren et al. 2003). Still,

little is known about the abiotic and biotic factors associated with these national-scale patterns of plant species distributions, or for other biological groups.

Realizing that exceptions exist, we surmise that native species richness is primarily controlled by optimal combinations of warm temperatures, high light, water, and nutrient availability (which we call ‘the good life’) – and by avoiding high stress, extreme environments. Currie (1991) and Rosenzweig (1995) do not discuss modern patterns of diversity resulting from the exponential exchange of species among continents and habitats. We were curious whether the richness and density patterns that have been observed between native and non-indigenous plant species (a pattern that supports local determinism) were generally observed among other taxonomic groups – namely birds and fishes. Human intervention (Mack et al. 2000), climate-matching (Venevski and Veneskaia 2003 for a review) or habitat-matching by non-indigenous species may be important prerequisites for successful invasion.

The role of modern humans in altering species distributions cannot be denied. Direct habitat loss and intentional invasive species introductions have been directly linked to human habitation (Soulé 1991a, b; Wilcove et al. 1998), and about 60% of humans live within about 170 km from the ocean or sea (Hindrichson 1997). Since the introduction of non-indigenous species is largely human-induced (via trade, modern transportation, and urbanization patterns), we included human factors in the list of potentially co-varying drivers of the patterns of non-indigenous species establishment. About 82% of the invasive non-indigenous woody plant species were escaped horticultural or agricultural products (Reichard 1997). Many non-indigenous plant seeds arrived as contaminants of forage crops (Reichard and White 2001). Native fishes were once moved in aquatic train cars from the eastern USA to the fish-poor lakes and streams in the west (Fuller et al. 1999), as well as those fish stocked with buckets atop mules or slung from helicopters. Inter-watershed canals, irrigation projects, and live-bait fisherpersons also facilitated the spread of non-indigenous fishes (i.e., fish from other ecosystems). Likewise, birds such as the feral pigeon or rock dove (*Columba livia*) have been

transported to the US since the early seventeenth century (Schorger 1952), various ‘game birds’ have been repeatedly stocked in most states, and escapes from the pet trade have facilitated the spread of species normally found in subtropical or tropical climates.

We propose that the observed relationships between native biodiversity and basic environmental covariates (Currie 1991; Rosenzweig 1995) should be observed among non-indigenous species because non-indigenous species would have adapted to similar environmental conditions in their countries of origin. Furthermore, non-indigenous richness may be predictable from native richness since the latter indicates optimal environments for growth and spread of non-indigenous species (Stohlgren et al. 2003). We realize that modern humans are the source of non-indigenous species propagules via trade and travel, and that land use practices and disturbance may facilitate the establishment, spread, and persistence of many non-indigenous species (D’Antonio et al. 1999). However, it may be that human populations are more instrumental in the initial establishment of invasions, and that environmental factors are more important in the spread and potential distributions of invasive species. If this were the case, then predictive models of the potential ‘habitat matching’ of invading species might be easily constructed from the same basic environmental factors (e.g., temperature, precipitation, elevation, latitude) that have been used to explain patterns of native richness and density.

We have the opportunity to assess preliminary trends in native and non-indigenous biodiversity with three large data sets on vascular plants, birds, and fishes throughout the United States. Our objectives were to (1) evaluate patterns of native and non-indigenous vascular plants, birds, and fishes at multiple spatial scales relative to environmental factors, human population, and cross-correlations among the biological groups; and (2) develop general models of non-indigenous species densities across multiple biological groups. We hypothesized that the densities of native species richness of each group would be positively and primarily associated with optimal environmental

conditions (low latitudes and elevations, warm temperatures, near coasts), while non-indigenous species densities would be positively associated with native species richness, optimal environmental conditions, and secondarily with human population and factors related to land use change.

## Materials and methods

### *Plant data*

The plant data set was gathered over the past 20 years by the Biota of North America Program (2002: <http://www.BONAP.org>) at the University of North Carolina, Chapel Hill. The taxonomic accuracy and completeness of the collection have made it the standard plant data set for many government and non-government agencies. The data set included the occurrence of over 24,000 native and 2770 non-indigenous plant taxa in 3074 counties in 49 states (excluding Alaska). Non-indigenous plant species were defined as those plant species with origins in other countries. This distinction is non-ambiguous and well accepted (<http://www.BONAP.org>). Non-indigenous records reflect all recorded introductions, including some species that have not been reported since being introduced. Due to incomplete data on current species distributions, we assumed that the patterns of past introductions are only a first approximation of current introduction patterns (a point we return to in the Discussion). To further protect against the influence of incomplete data in some counties, all records with fewer than 100 native plant species were removed from analysis, leaving 3004 counties (over 95%) in the sample.

### *Fish data*

Data on native and non-indigenous fish species were collected from NatureServe's database (on-line at <http://www.natureserve.org/explorer/>) and the USGS Florida Integrated Science Center's Non-indigenous Aquatic Species Database, respectively. Aquatic species data are commonly organized by Hydrologic Unit Code (HUC), a hierarchical system of drainages that become

increasingly smaller as the resolution increases. Both databases were originally compiled at the 8-digit HUC, but were converted to the 6-digit HUC scale because the non-indigenous fish data were more complete at this coarser resolution. The NatureServe database contained 782 native fish species in 329 drainages (6-digit HUC) across 50 states. Analysis was completed on the 328 drainages that contained data for both native and non-indigenous species. The Non-indigenous Aquatic Species Database included 672 species in 337 drainages across 50 states. Non-indigenous fishes included all introductions of fishes foreign to local or regional drainages including lake trout introductions to Yellowstone Lake in Wyoming, and tropical aquarium fish introductions to southern reservoirs. Many but not all of these species introductions have resulted in reproducing populations or have persisted for several years based on multiple reports of occurrence. Only introductions not specifically known to have failed, and those introductions that have not been eradicated were included in the analysis.

### *Bird data*

Native and non-indigenous bird data were compiled at the USGS Patuxent Wildlife Research Center, producing species richness data for 3079 counties across 50 states (Alaska not shown). For 36 states, distribution data were obtained from published breeding bird atlas projects conducted between the mid-1970s and late 1990s. Various state and regional publications provided distribution information for states lacking published atlases. The dataset for non-indigenous birds totaled 107 species that are either not native to North America or have been introduced outside of their original North American range, such as Canada goose (*Branta canadensis*) and house finch (*Carpodacus mexicanus*) in the eastern states. Species escaping from captivity were included only if successfully reproducing populations have been established.

### *Environmental data and human factors*

Geographic variables included latitude, longitude, distance to coast, mean elevation and

variation in elevation in a county, county area, and drainage area (Appendix A). Environmental variables included mean minimum temperature, mean annual temperature, mean annual precipitation, potential evapotranspiration (PET; see Thornthwait and Mather 1955; WeatherDisc Associates 1990), and potential vegetation carbon. Human factors included human population, road density, % cropland in a county, and an index of habitat disturbance (ratio of area disturbed [developed, cultivated, and surface mines] to total county area). Habitat heterogeneity was not directly measured. Factors associated with habitat heterogeneity as reported in the literature include plant species richness and variation in elevation (see Rosenzweig 1995).

#### *Statistical analysis*

The relationships (state, county, and drainage distributions) between native and non-indigenous species richness within taxonomic groups were evaluated with correlations. At the state-level, we correlated the richness of native and non-indigenous plant species to human population data, and correlated densities of native and non-indigenous plant species as a basis for our more specific objectives to evaluate the environmental factors associated with invasions at county-level scales. We then evaluated the three taxonomic groups with biotic and abiotic variables to quantify relationships between species richness and environmental data (see Appendix A), and to predict the richness and densities of non-indigenous species for each group. Combining disparate datasets involved sub-sampling county-level, HUC-level data, and environmental data for each of the 3004 counties with 100 or more native plant species throughout the conterminous United States and Hawaii using GIS software (ESRI, ArcView 3.2). Each point was drilled through the county's geographic centroid, and various data layers recorded for that location. The resulting matrix aligned data at unique locations and allowed us to examine the relationships of biotic and abiotic data collected at various scales. Data not normally distributed were transformed prior to statistical analyses. We used a square-root transformation

for human population data and statewide density data, and log-transformations ( $\log_{10}X + 1$ ) on native and non-indigenous plant species, native and non-indigenous fish and bird data, elevation (m), range in elevation in a county, and mean vegetation carbon ( $\text{gC/m}^2$ ). Response variables included native and non-indigenous taxa richness (i.e., per county or HUC), and native and non-indigenous taxa density ( $\# \text{ species/km}^2$ ; mean density in the county or HUC).

Because of the tremendous variation in the sizes of counties and drainages, we evaluated patterns of diversity in three ways. Raw species richness values by county (for plants and birds) or by drainage HUC (for fish species) were mapped to compare national patterns of native vs non-indigenous species. Then we mapped the proportion of non-indigenous species by county to eliminate the effect of area in the comparisons for each biological group. Because the strict use of proportional data can mask large differences in species richness and densities among biological groups across the U.S., we further investigated models of species densities. Preliminary species–area analyses showed that for all biological groups, ‘area’ explained little of the variation in species richness ranging from a high of 16% for native plants species/county to  $<0.1\%$  for non-indigenous plant species/county using simple linear regression models. We also evaluated species– $\log_{10}$ area curves (i.e., semi-log relationships) for biological groups for native and non-indigenous species, but in each case, the amount of variation explained was equal or less than the simple linear species–area relationship. Therefore, we used density ( $\# \text{ species/km}^2$ ) in subsequent analyses. Because two-thirds of species–area tests were significant, albeit weak, we emphasize the statistical relationships among taxa densities. Significant values in all cases were determined using the SYSTAT statistical software (Version 10, 2000). We eliminated latitude, longitude, and distance to coast in multivariate models in favor of proximate factors associated with diversity (e.g., PET, vegetation carbon, minimum temperature). Adjusted  $R^2$  values are presented for all multivariate models.

## Results

### *The geographic setting and state-level patterns*

Understanding the geography and topography of the continental USA helped set the stage for evaluating patterns of species diversity. Data from the 3004 county centroids detailed the geographic setting and showed that as latitude increased from Mexico to Canada, mean annual temperature sharply declined ( $r=-0.91$ ), and mean annual precipitation declined ( $r=-0.42$ ; Table 1) with exceptions, no doubt, in mountainous areas. Due to the shape and topography of the USA, increasing latitudes coincided with increasing distance to coastlines ( $r=0.54$ ) and increasing mean elevation ( $r=0.48$ ; Table 1). Increasing longitude (moving east to west in the USA) coincided with slightly rising temperatures

( $r=0.13$ ) and precipitation ( $r=0.51$ ; longitude is not shown in Table 1).

The geography and topography of the USA translate into generalized patterns of potential evapotranspiration, which is negatively correlated to latitude ( $r=-0.91$ ), and estimates of the potential total carbon stored in vegetation, which is positively correlated to precipitation ( $r=0.74$ ), mean annual temperature ( $r=0.30$ ), and PET ( $r=0.24$ ). While all the above correlations were significant ( $P<0.0001$ ), they explain only a modest amount of the natural variability of a complex landscape that includes steep mountains with rain shadow effects, large lakes and estuaries that moderate temperatures, broad valleys, and deserts. In addition, intermittent ice ages and climate change may contribute to historic and current patterns of native diversity.

*Table 1.* Cross-correlations of the density of native and non-indigenous plant and bird species (county-level densities; # spp./km<sup>2</sup>) and native and non-indigenous fish species (6-digit HUC-level densities; # spp./km<sup>2</sup>) with environmental factors and human factors (on log-transformed data) for 3004 counties in 49 states (excludes Alaska). ns = not significant at  $P<0.05$ .

	Nat. plant	N-I plant	Nat. bird	N-I bird	Nat. fish	N-I fish	Latitude	Mean temp.
Nat. plant	1.00							
N-I plant	0.86	1.00						
Nat. bird	0.78	0.80	1.00					
N-I bird	0.71	0.81	0.93	1.00				
Nat. fish	0.30	0.16	0.24	0.17	1.00			
N-I fish	0.39	0.35	0.31	0.29	0.34	1.00		
Latitude	ns	0.09	ns	ns	-0.18	-0.11	1.00	
Mean temp.	ns	ns	ns	ns	0.18	0.06	-0.91	1.00
Precip.	0.32	0.15	0.24	0.15	0.47	0.20	-0.42	0.45
PET	ns	-0.10	ns	ns	0.17	ns	-0.91	0.94
Elev.	-0.33	-0.27	-0.29	-0.25	-0.36	-0.13	0.48	-0.57
Dist. coast	-0.25	-0.22	-0.20	-0.14	-0.14	-0.37	0.54	-0.58
Veg. C	0.46	0.26	0.34	0.23	0.50	0.27	-0.32	0.30
Hum. pop	0.59	0.70	0.56	0.65	0.16	0.39	ns	ns
Road den.	0.54	0.58	0.46	0.50	0.16	0.31	-0.10	0.14
Crop %	-0.44	-0.39	-0.48	-0.41	-0.16	-0.36	0.24	-0.16
Hab. dist.	0.12	0.15	0.12	0.17	0.08	-0.18	0.24	-0.15
	Precip.	PET	Elev.	Dist. coast	Veg. C	Hum. pop	Road den.	Crop %
Precip.	1.00							
PET	0.41	1.00						
Elev.	-0.58	-0.61	1.00					
Dist. coast	-0.54	-0.56	0.67	1.00				
Veg. C	0.74	0.24	-0.49	-0.45	1.00			
Hum. pop.	0.15	ns	-0.28	-0.29	0.23	1.00		
Road den.	0.21	0.10	-0.24	-0.25	0.29	0.85	1.00	
Crop %	-0.35	-0.10	0.18	0.46	-0.39	-0.41	-0.32	1.00
Hab. dist.	-0.11	-0.10	-0.11	0.38	-0.07	0.16	0.25	0.56

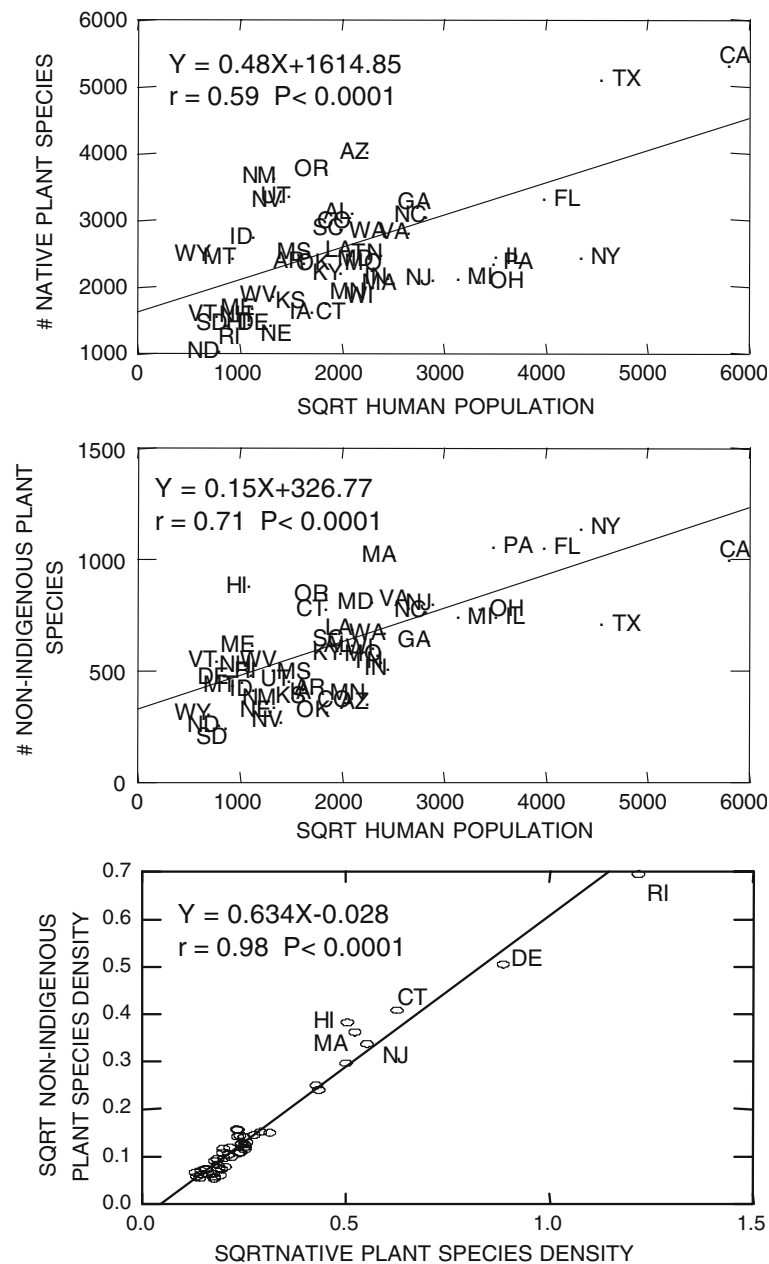


Figure 1. Relationship between statewide human population (square-root transformed data) and native plant species richness (top) and non-indigenous species richness (middle), and the relationship between the density of native plant species and the density of non-indigenous plant species in a state (bottom).

Modern humans have tended to settle in species-rich areas with favorable climates and natural amenities (Chown et al. 2003; Luck et al. 2004; Gaston and Evans 2004). At state-wide scales, there was a strong positive relationship between native plant species richness and human

population (square-root transformed data;  $r = 0.59$ , Figure 1). Since native plant diversity probably established long before human settlement (Stebbins and Major 1965), we can infer that environmental factors were the proximate factors of plant species richness. An even

stronger positive relationship between human population and non-indigenous plant species richness ( $r=0.71$ ; Figure 1; also see Rejmánek 2003) could be direct evidence of human trade, cultivation, accidental introductions, or human-assisted establishment in a subset of populated areas and spread to others. However, while human population was correlated to both native and non-indigenous plant species richness, both relationships are influenced by the area of the state (i.e., larger areas generally contain more humans and species than smaller areas with similar environments). When the effect of area is removed by assessing human population density ( $\#/km^2$ ) and species density ( $\# \text{ species}/km^2$ ), the positive correlations improved for native plant species density ( $r=0.74$ ;  $P<0.0001$ ) and non-indigenous plant species density ( $r=0.76$ ;  $P<0.0001$ ). Interestingly, there was an even stronger positive correlation between native and non-indigenous plant species density ( $r=0.98$ ;  $P<0.0001$ ; Figure 1), corroborating the notion that the native and non-indigenous plants species may be responding to similar environmental variables. In addition, at state-levels, 54% of the variation in the density of non-indigenous fish species per state could be explained by the positive relationship with the density of native fish species per state ( $P<0.0001$ ). Higher resolution information on human populations and species diversity may help to distinguish relative importance of human factors from environmental factors related to plant diversity and invasion patterns.

#### *General patterns of native and non-indigenous species richness in the USA*

On average at the state-level, non-indigenous plant species enrich the flora by  $26\% \pm 1\%$ , while non-indigenous fish species enrich the fish faunas by  $58\% \pm 23\%$ . Hawaii and Arizona added 27 fish species where three were native. In addition, at state levels, the density of native plant species was significantly positively correlated to the density of native fish species ( $r=0.85$ ,  $P<0.0001$ ), non-indigenous plant species ( $r=0.79$ ,  $P<0.0001$ ), and non-indigenous bird species density ( $r=0.90$ ,  $P<0.0001$ ).

At the HUC drainage level, fish faunas were increased by  $121\% \pm 16\%$  by non-indigenous species introductions. On average at the county-level, non-indigenous plant species enrich the flora by  $13.9\% \pm 0.1\%$ , while non-indigenous bird species enrich the bird fauna by  $6.7\% \pm 0.1\%$ . County-level patterns of native and non-indigenous plant species richness (Figures 2a, b) revealed areas of especially high richness in the west, southwest, Gulf Coast, and New England areas – for both native and non-indigenous species. Hawaii had a moderate number of native plant species, but very high non-indigenous plant species richness. Some areas contained noticeably limited data, such as Texas, Georgia, Mississippi, and parts of the Dakotas. The patterns show no bias in reporting native and non-indigenous species for counties with higher species richness, but we confined our statistical analysis to the 3004 counties with 100 or more native plant species recorded.

Assessing the proportion of non-native species in a county or watershed effectively removes the ‘area’ effect when comparing patterns of invasion. The ratios of non-native plant species in counties revealed hotspots of successful establishment in Hawaii, fertile valleys in the Pacific Northwest, coastal and Central California, and throughout the northeastern USA (Figure 2c). Some areas high in native species richness (Figure 2a) were high in the proportion of non-native plant species (Figure 2c), such as in the northeastern U.S.A. and Pacific Coast areas. Conversely, some areas low in native species richness (Figure 2a) had high ratios of non-native plant species (Figure 2c), such as in Montana and portions of the Pacific Northwest. In general, counties high in non-native species richness (Figure 2b), often had high ratios of non-native plant species, such as the northeastern USA, Pacific Coast, and Pacific Northwest.

Patterns for native bird species richness revealed high richness counties concentrated among Pacific Coast states and the northern Rocky Mountains (Figure 2d). The southeast USA generally had fewer native bird species per county than the northeast USA. Non-indigenous bird species richness also was high near the southern Oregon–California boundary, very high in Hawaii, high in corn producing areas, and near Miami and Los Angeles (Figure 2e). The hotspots near the two cities may reflect pet-trade escapes or



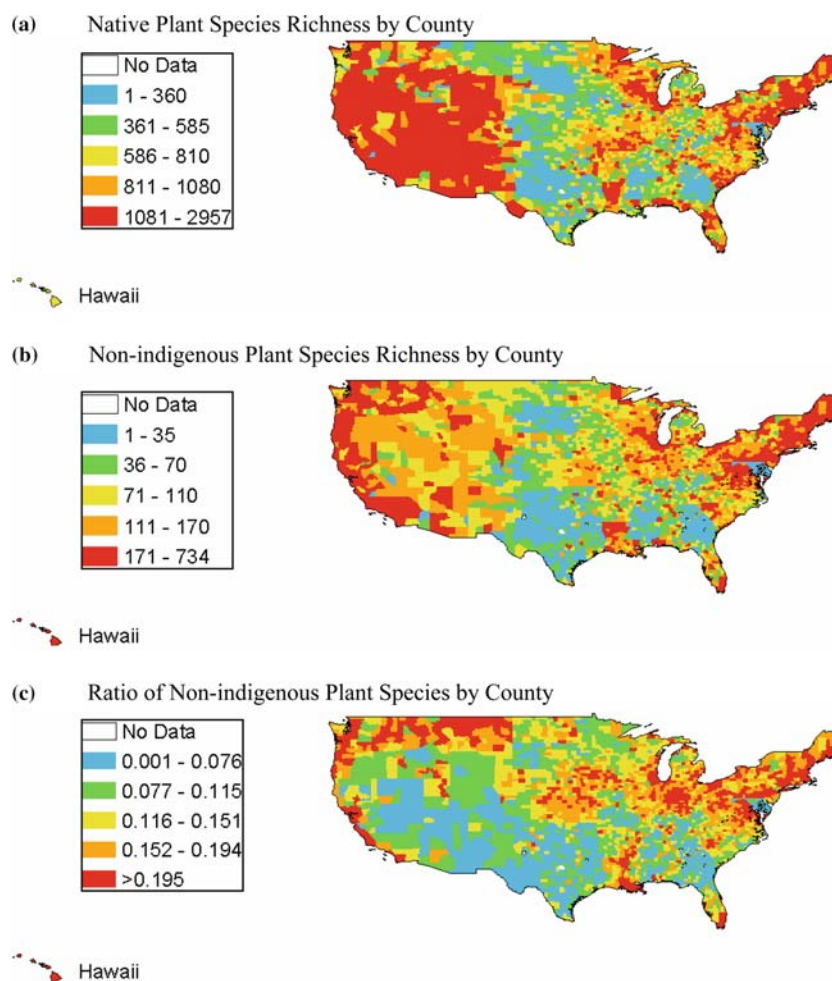


Figure 2. Patterns of (a) native and (b) non-indigenous plant species richness by county; (c) the ratio of non-indigenous plant species by county; native (d) and non-indigenous (e) bird species richness by county; (f) the ratio of non-indigenous bird species by county; native (g) and non-indigenous (h) fishes by HUC drainage; and (i) the ratio of non-indigenous fishes by drainage (see Materials and methods and Appendix A for data sources).

releases of tropical species. Ratios of non-indigenous bird species in counties showed hotspots of successful establishment in Hawaii, Florida, and the portions of the Midwest and Central Grasslands that are associated with corn production (Figure 2f). Large areas in the western USA were high in native species richness (Figure 2d) but had low ratios of non-indigenous bird species. In general, counties low in native and non-indigenous bird species richness (Figures 2d, e), often had slightly higher ratios of non-indigenous bird species (Figure 2f).

Patterns of native fish richness show the distinct hotspot in the Mississippi valley region, with

sharp gradients in native species richness to the east and west (Figure 2g). The western states had modest inland fisheries. Data on non-indigenous fishes are still being gathered, but preliminary patterns from 328 drainages suggest hotspots in Hawaii, southern Florida, and southern California/Arizona (Figure 2h). Another obvious pattern is that non-indigenous fish have been actively transported and stocked throughout the USA. Thus, the ratios of non-indigenous fish species in watersheds showed hotspots of successful establishment in the western USA, Hawaii, Florida, and the Great Lakes region (Figure 2i). These hotspots are the opposite of native fish hotspots in the

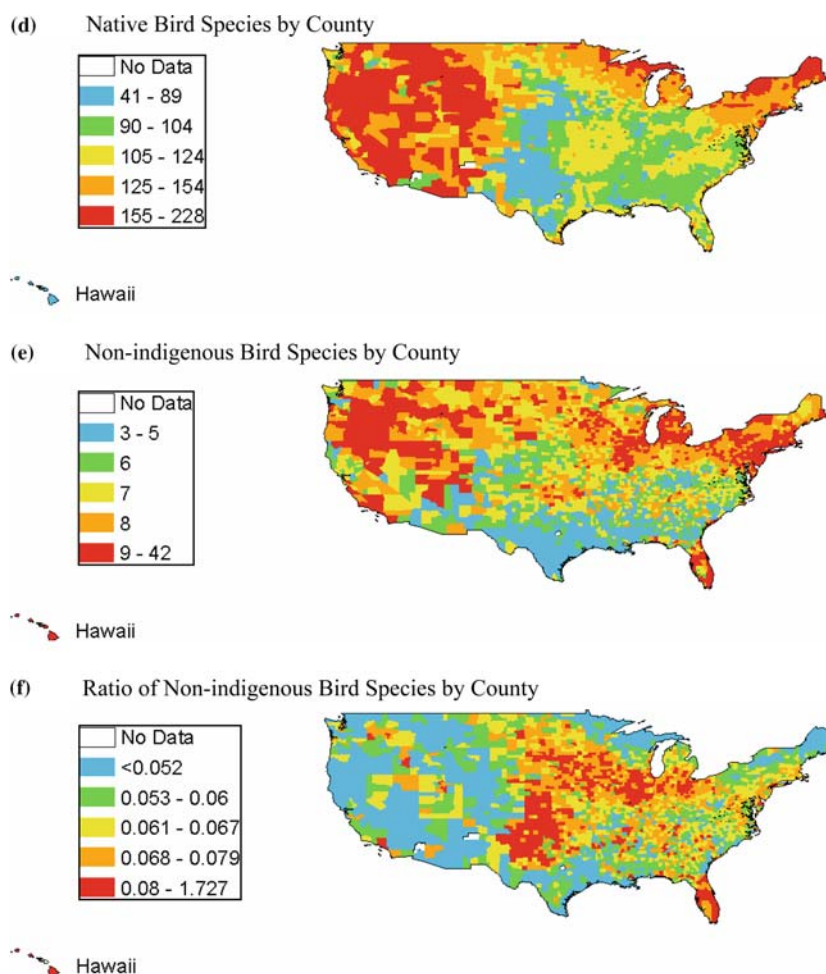


Figure 2. Continued.

Mississippi Valley (Figure 2g), and often matched the patterns of non-indigenous fish introductions (Figure 2h).

*Relationships of native to non-indigenous species richness within taxa*

We found that native plant species richness was a significant positive predictor of non-indigenous plant species richness (Figure 3a), and that the densities of native and non-indigenous plant species richness were more strongly positively correlated (Figure 3b). Likewise, for 3074 counties in 49 states, native bird species richness was a strong positive predictor of the richness of non-indigenous birds in a county

(Figure 3c), with a stronger positive correlation between densities (Figure 3d). For the 328 HUCs in 49 states (excluding Alaska), the richness of native fishes was not significantly correlated with non-indigenous fish richness (Figure 3e), but there was a significant positive relationship between native and non-indigenous fish species densities (Figure 3f).

*Biotic and abiotic factors associated with the density of native and non-indigenous species richness*

Stepwise multiple regression models identified many biotic, abiotic, and human factors that could strongly predict the density of native species

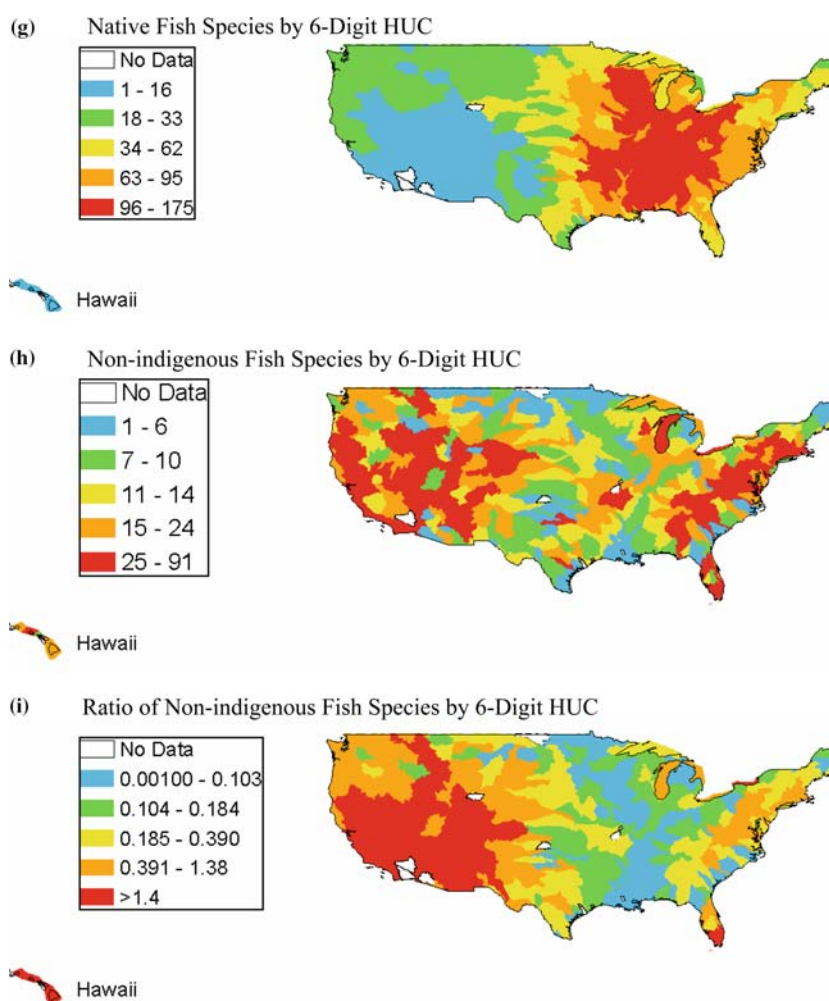


Figure 2. Continued.

(Table 2). The strongest predictors of the density of native plant species were positive relationships with the density of native bird species ( $S_b = 0.51$ ) and vegetation carbon ( $S_b = 0.19$ ), and a negative relationship with PET ( $S_b = -0.20$ ). To a lesser extent, the density of native plant species was positively correlated with minimum temperature, road density, the range in elevation, and the proportion of disturbed lands in a county. The density of native plant species richness was positively associated with mean annual precipitation in simple correlations, but negative in the multiple regression (Table 2). The multiple regression model that included road density and the proportion of disturbed lands in a county explained 66% of the

variation in the density of native plant richness. Without the human factors in the model, 67% of the variation was explained (Table 2).

The density of native bird species richness also could be well predicted from a mix of environmental and human factors ( $R^2 = 0.66$ ; Table 2). The density of bird species richness was primarily positively associated with the density of native plant species richness ( $S_b = 0.53$ ), and lesser contributions from crop area, PET, human population, and other factors (Table 2). There was only a slight change in model results when crop area, disturbed lands, human population, and road density were excluded from the model ( $R^2 = 0.62$ , Table 2).

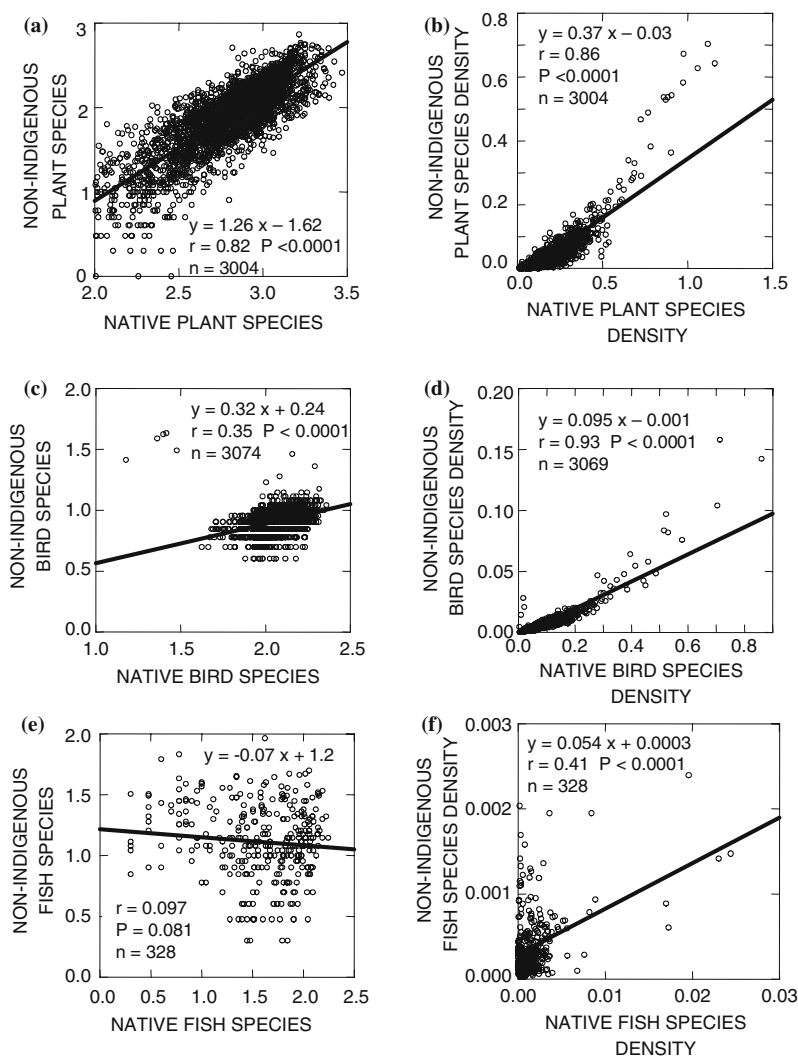


Figure 3. Relationships of native to non-indigenous plant species richness in counties (a) and native and non-indigenous plant species density (mean # species/km<sup>2</sup>) in counties (b), native to non-indigenous bird species richness in counties (c) and native and non-indigenous bird species density (mean # species/km<sup>2</sup>) in counties (d); native to non-indigenous fish species richness in drainages (e) and native and non-indigenous fish species density (mean # species/km<sup>2</sup>) in drainages (f). All data were log<sub>10</sub> transformed (log<sub>10</sub> X + 1).

The weakest predictive model was for the density of native fish species in HUCs ( $R^2=0.31$ , Table 2), driven largely human intervention and the coarse resolution of the fish data ( $n=334$  drainages) relative to the county-level data (3004 counties). The model reflected positive associations with vegetation carbon and precipitation, and a negative association with the range in elevation in a county. All the human factors including cropland area, percent disturbed lands, road

density, and human population were selected variables in the stepwise multiple regression. However, when the human factors were removed from the model, it explained the same amount of variation in the density of native fish species per HUC (Table 2).

Stepwise multiple regression models were stronger for the density of non-indigenous plant species richness than for native plant species ( $R^2=0.84$ , Table 3), largely driven by the very

Table 2. Multiple regression results for density of native plant and bird species (county-level densities; # spp./km<sup>2</sup>) and native fish species (HUC-level densities; # spp./km<sup>2</sup>) in the USA ordered by the standardized partial regression coefficients (in parentheses).

Priority predictor	Native plants	Native birds	Native fishes
1	Den. nat. birds (0.51)	Den. nat. plants (0.53)	Veg. carbon (0.30)
2	PET (-0.20)	Crop area (-0.38)	Range elev. (-0.26)
3	Veg. carbon (0.19)	PET (-0.29)	Precip. (0.23)
4	Road den. (0.17)	Human pop. (0.22)	Elev. (0.16)
5	Min. temp. (0.15)	Road density (-0.22)	Road density (-0.14)
Others	Range elev. (0.12), Disturb. land (0.07), Crop area (-0.06), Precip. (-0.05)	Disturb. land (0.21), Range elev. (-0.17), Mean temp. (0.14), Min. temp. (0.11), Elev. (0.05), Veg. carbon (-0.05)	Human pop. (0.14), Den. nat. plants (0.11), Crop area (0.04)
Adj. $R^2$	0.66	0.66	0.31
Adj. $R^2$ w/o human factors	0.67	0.62	0.31

Table 3. Multiple regression results for density of non-indigenous plant and bird species (county-level densities; # spp./km<sup>2</sup>) and non-indigenous fish species (HUC-level densities; # spp./km<sup>2</sup>) in the USA ordered by the standard partial regression coefficients (in parentheses).

Priority predictor	Non-indigenous plants	Non-indigenous birds	Non-indigenous fishes
1	Den. native plants (0.64)	Den. native birds (0.93)	Range elev. (0.43)
2	Human pop. (0.33)	Human pop. (0.33)	Den. nat. fish (0.33)
3	Veg. carbon (-0.11)	Road dens. (-0.15)	Human pop. (0.23)
4	Road density (-0.10)	Elev. (0.11)	Elev. (-0.22)
5	Elev. (-0.09)	PET (0.10),	Den. nat. plants (0.19)
Others	Crop area (0.07), Range elev. (0.06), Precip. (-0.05), Den. Nat. Fish (-0.04), Disturb. land (-0.02)	Range elev. (-0.07), Crop area (0.07), Veg. carbon (-0.04), Min. temp. (-0.04), Den. nat. plants. (-0.04), Den. nat. fish (0.03)	Disturb. land (-0.10), Precip. (-0.07), min. temp. (0.06), Den. nat. bird species (0.02)
Adj. $R^2$	0.84	0.91	0.38
Adj. $R^2$ w/o human factors	0.82	0.89	0.34
$R^2$ w/o predictor 1 only	0.75	0.87	0.11

strong positive relationship between the densities of native and non-indigenous plant species richness. The model included 10 factors, but native plant species densities alone would have explained 75% of the variation in the density of non-indigenous plants. Without the human factors, 82% of variation was explained by the model.

The strongest multiple regression model explained 91% of the variation in non-indigenous bird species density primarily driven by the significant positive relation with the density of native bird species ( $S_b=0.93$ ). Human population density and nine other factors contributed far less to the model (Table 3). Roughly the same amount of variation could be explained without

the human factors, and 87% of the variation could be explained by including only the density of native bird species.

The predictive models for non-indigenous fishes explained 38% of the variation in the density of non-indigenous fishes, and 34% without human factors (Table 3). The density of native fish species was a significant positive predictor of the density of non-indigenous fishes in a HUC in simple regressions.

The densities of all three native species groups had highly significant positive relationships with the other species groups (Table 1), and the models were influenced by several environmental factors (Table 2). The multivariate models of the densities of all three non-indigenous groups had

strong positive relationships with the densities of their native species group (Table 3). However, many of the same factors helped to explain the densities of native and non-indigenous within the species groups.

## Discussion

### *Local determinism, evolutionary history, and patterns of native biodiversity*

Local determinism may play an extremely important role in the richness and densities of native plant, bird, and fish species. Native species densities were significantly positively correlated to precipitation and potential vegetation carbon storage, and significantly negatively correlated with elevation and distance to coast (Table 1). This is growing evidence that a few environmental factors may control species richness at global (Currie 1991; Huston 1994; Rosenzweig 1995; Kleidon and Mooney 2000; Allen et al. 2002; Hawkins et al. 2003), continental and regional (this study), and landscape-scales (Stohlgren et al. 1997, 2002; Chong et al. 2001). Equally important, we found that native plant, bird, and fish species densities were positively cross-correlated suggesting that multiple biological groups may track each other in predictable ways (Currie 1991; Tables 1 and 2). Native plant and bird species densities in the U.S. can be explained by favorable environmental conditions ( $R^2=0.66$ ; Table 2) coinciding with well-documented global patterns of diversity (Currie 1991; O'Brian 1998; Francis and Currie 2003; Hawkins et al. 2003). It is reasonable to expect that native species in other groups may benefit from these same environmental factors (e.g., pollinators and terrestrial invertebrates; Turner et al. 1987, 1988).

Evolutionary history also may play a significant role in native biodiversity (Flather et al. 1998). Native fish species were prominent in the drainages of the Mississippi River (Figure 2g). High endemic areas of freshwater fishes also coincide with the unique geologic history of the southern Appalachians (Williams et al. 1989; Warren and Burr 1994). Likewise, California has an overwhelming abundance of total species and

endemic species (Dobson et al. 1997), in part due to its unique paleo-biogeography (Stebbins and Major 1965), high habitat heterogeneity, large area, and abundant soil and water resources in many areas (see Stein et al. 2000). This mimics global patterns where some areas of high plant diversity or endemism are associated with 'specific ecological and evolutionary features' (Gentry 1986; Venevski and Veneskaia 2003) including arid landscapes with infertile soils such as the fynbos region of South Africa (Bond 1983; Cowling et al. 1998) and southwest Australia (Abbott 1977; Abbott and Black 1980), and in the southwestern USA (Dobson et al. 1997). However, most hotspots of plant endemism and diversity are more closely associated with tropical and subtropical areas with abundant solar radiation and rainfall (Rosenzweig 1995; Myers et al. 2000).

Disturbance history may also influence broad patterns of native diversity. Very productive, long-undisturbed sites dominated by full-canopy trees (e.g., Norse 1990) may have low understory plant and bird diversity. At fine scales, some wetland habitats can be dominated by a few plant species, despite generous available resources, but even these botanically poor sites can support high diversity of birds, fishes, and other organisms (Brinson and Malvárez 2002). However, because disturbances such as fires, insect and disease outbreaks, floods, small mammal diggings, etc., are so ubiquitous in most ecosystems, long-undisturbed sites may be rare (in terms of area) or patchy at county scales.

### *Local determinism, recent history, and patterns of non-indigenous biodiversity*

Three lines of evidence support the hypothesis that local determinism also may play an extremely important role in the richness and densities of non-indigenous species. First, there were strong within-taxa and across-taxa correlations between densities of native and non-indigenous plant, bird, and fish species (Tables 1 and 3). Second, like their native species counterparts, non-indigenous species generally tracked the same environmental factors in a consistent way (Table 1). Third, the multivariate models performed equally well with or without human

factors included. The lesser role of local determinism for non-indigenous fishes is likely due to the role of modern humans in subjectively stocking estuaries, rivers, streams, and lakes in the USA (Fuller et al. 1999) and the coarse resolution of the fish data. 'Recent history' and dispersal limitation may play more important roles than local determinism and evolutionary history in non-indigenous fish distributions.

Patterns of non-indigenous plant and bird species diversity were even more predictable than their native counterparts (Tables 2 and 3). This may be because native species have had a longer evolutionary time to become established and spread to a wider range of productive to stressful habitats compared to non-indigenous species, or because the non-indigenous species include only a subset of plant families and genera with more specific habitat requirements (Rejmánek 1999; Mack et al. 2000). However, with 84 and 91% of variation explained in patterns of non-indigenous plant and bird species densities, the potential importance of local determinism should not be underestimated (Table 3). Such models are a logical first step in identifying areas in immediate need of multi-species control and restoration activities to protect native diversity (Stohlgren et al. 2003). Our results provide further support for the 'the rich get richer' hypothesis (Stohlgren et al. 2003). For example, California, Arizona, New York, and Florida and other areas high in endemism (Dobson et al. 1997) are also hotspots of native species richness and invasions (Figure 2). Species-rich, productive estuaries are especially well invaded in the USA (Cohen and Carlton 1998), however, areas initially poor in fish species (e.g., Arizona), also have been well invaded by non-indigenous fish species (Fuller et al. 1999).

There was some evidence that as native plant and bird species densities increased, non-indigenous species densities increased at an even faster rate (Figures 3b, d). At the highest levels of native species' densities, the densities of their non-indigenous species counterparts were well above the regression line. This may suggest that the very rich get even richer. Along with the state-level patterns (Figure 1), and the highly positive cross-correlations among the densities of native and non-indigenous species

of the three biological groups at county-levels (Tables 1 and 3), our results continue to suggest that biotic resistance and competition from native species may be weak forces in the establishment of non-indigenous species at landscape-, county-, drainage-, and state-levels (Stohlgren et al. 1999a, 2002, 2003, this study).

#### *Why do the rich get richer?*

Identifying specific mechanisms and processes associated with invasion is beyond the scope of this correlative study. However, multiple-scale observations of native biodiversity and invasion may help generate hypotheses for experiments and theoretical models (Stohlgren 2002). There are many potential causes for the success of non-indigenous species in species-rich areas including climate and habitat matching, weak competition for resources from native species, use of previously under-used resources, open niches, or escape from natural predators (see Mack et al. 2000). Native and non-indigenous species may simply be responding to similarly inviting habitats and resources (this study), coexisting due to habitat heterogeneity (Huston 1994), high species turnover, increased pulses of available resources from continued large and small disturbances (D'Antonio et al. 1999), and thus, more opportunities for the establishment of non-indigenous plants (Abbott 1977; Abbott and Black 1980; Rosenzweig 1995; Stohlgren et al. 1997, 1999a, b, 2003). This appears to be the case for plants in Rocky Mountain National Park, Colorado, in the Central Grasslands of the USA (Stohlgren et al. 1999a, 2002), and across the USA (Stohlgren et al. 2003, this study).

The simplest explanation of the general patterns on non-indigenous species is that they evolved in their original habitats and continents under similar environmental constraints. For example, Brazilian pepper tree, Australian melaleuca, and Asian cogongrass were pre-adapted to the climatic conditions they found in Florida. The European brown trout has similar habitat requirements to many native trout species and subspecies. Thus, it should not be surprising that climate matching (Venevski and Veneskaia 2003) and habitat matching in non-indigenous species are consistent with well-established global



patterns of native diversity (Huston 1979, 1994; Currie 1991; Rosenzweig 1995).

While the processes of invasion across spatial scales remain elusive (Stohlgren et al. 2002), the patterns of invasions may be becoming more general and predictable. Overwhelmingly, California and other species-rich states and counties in favorable climates have also been successfully invaded by multiple biological groups (Figures 1–3). Despite no direct cause–effect relationship between native and non-indigenous species richness (Levine and D’Antonio 1999; Levine 2000; Lonsdale 1999; Rejmánek 1996, 1999), the strongly positive statistical relationships are cause for concern (Tables 1–3). High native species richness and density often are directly linked to productive or moderately productive environments (e.g., various combinations, warm temperatures, high precipitation, high PET, low elevations, southerly latitudes, close to the coast, etc.; Tables 1–3).

The Hawaiian Islands, and other archipelagoes, are famed exceptions to the rich get richer pattern of invasions, presumably due to lack of competition and predators and favorable environments (Elton 1958; but see Rejmánek 1996). Other exceptions include Montana for plants (Figures 2b, c), Oklahoma for birds (Figures 2e, f), and the entire western USA for fishes (Figures 2h, i). However, for much of the land base in the USA, many species-rich areas in the USA are being invaded by hundreds or thousands of species (Figures 1–3).

#### *Re-evaluating the role of humans in the invasion process*

At coarse state-levels, human population is a strong correlate to native diversity (but perhaps not a forcing factor) – environmental factors may be more proximate predictors. Humans settled in species rich, high productivity warm sites, with slightly lower populations in the most productive sites (used for agriculture and forestry) and significantly lower populations in inhospitable climate areas (Figure 1a). At county levels, human factors such as human population, percent cropland, road density, and percent disturbed lands in a county were weakly but positively associated with native and non-indigenous species in the

three taxonomic groups. However, the predictive models performed similarly well without the human factors included. Humans are continual importers of non-indigenous species and active transporters of organisms (Reichard and White 2001; Mack et al. 2000), and especially for fishes (Kolar and Lodge 2002).

Human populations, commerce, and transportation networks provide ample pathways for intentional and unintentional introduction of non-indigenous species (Reichard and White 2001). Once introduced, many non-indigenous species spread by various means to suitable habitat sometimes very distant from the point(s) of introduction (e.g., phragmites, starlings, brown trout). The final distributions of non-indigenous species may be primarily determined by environmental factors – much like their native species counterparts (Tables 1–3; Figures 1–3).

Species often spread far beyond the area they were released. For example, *Poa pratensis* (Kentucky bluegrass) escaped well into riparian zones in Wind Cave National Park, South Dakota (Stohlgren et al. 1999b), and birds widely disperse seeds and fruits of non-indigenous plants, and freshwater trout move up or downstream from points of introduction. We expect that the vulnerability of habitats to invasion, species traits, and propagule availability or abundance must be important in the spread of species once introduced. Humans will continue to facilitate the movement of many species, especially as global trade increases, and species adaptations and changing environmental factors will continue to effect the potential distribution of many non-indigenous species. Thus, it will be increasingly challenging to predict species’ potential distribution and subsequent environmental and economic effects (Schnase et al. 2002). Where environmental and economic effects are unknown or poorly understood, every effort should still be made to limit the introduction of species with broad ‘potential’ environmental ranges. We realize that most non-indigenous species fail to successfully establish, and few species are highly invasive, but the probability of successful invasion will increase with the total number of species freely admitted.

Humans may alter disturbance regimes (e.g., fire, flooding, soil disturbance) to further facilitate



invasions. However, many fairly undisturbed areas have been successfully invaded such as ungrazed grassland sites, tree-canopy gaps, small-mammal mounds, and plant deaths throughout many natural areas (Stohlgren et al. 1999a, b). Pathogens such as Dutch elm disease, Chestnut blight, blister rust, whirling disease, and West Nile Virus also have forcefully invaded disturbed and undisturbed ecosystems with a vengeance.

### Conclusions, recommendations, and future directions

Each of our data sets could be improved, as could the ancillary data layers used in modeling and the models themselves. However, this is the first attempt to evaluate patterns of native and non-indigenous vascular plants, birds, and fishes at multiple spatial scales relative to environmental factors, human population, and cross-correlations among the biological groups. Additional data on plant species richness are needed for many counties in the USA (i.e., those with less than a few hundred native plant species seem suspiciously low). The bird data only included breeding birds, and patterns during non-breeding seasons may help to understand the interactions of non-indigenous species with their environment. Additionally, the development of an electronic breeding bird atlas database may improve our understanding of relationships at smaller geographic scales. Non-indigenous fish data have not all been refined to the 8-HUC (Hydrologic Unit Code) drainage scale. Additional data at higher resolutions will be helpful in refining spatially predictive models of species richness and density. Of course, we also need to more closely link richness and density to abundance, cover, and dominance, and to link species-level data to habitat quantity, quality, and connectedness by roads and waterways (i.e., corridors of invasion) and barriers to invasion. Still, we can identify several tentative conclusions and areas requiring additional research.

We conclude, as hypothesized, that native species richness of each group would be positively and primarily associated with optimal environmental conditions (low latitudes and elevations, near coasts), while non-indigenous

species richness would be positively associated with native species richness, optimal environmental conditions, and secondarily with human population and factors related to land use change. These patterns echo observed patterns of native biodiversity from landscape to global scales (e.g., Currie 1991; Rosenzweig 1995).

We recommend a broader definition of 'prevention' in the USA that includes preventing species from expanding from their initial ports of entry to other destinations then to vulnerable habitats far removed from the original points of initial entry. Areas that continue to receive high numbers of introductions and subsequent relocations (via inter-continental trade, transportation) combined with natural spread to additional habitats – may soon lead to many non-indigenous species finding and exploiting suitable habitats. Many national parks, wildlife refuges, counties, and states would benefit from prevention programs similar to those at our primary ports and airports.

We recommend additional research on the environmental, geographic, and human factors associated with species invasions. Predictive models may be improved by using many of the factors identified here (Tables 1–3) and finer resolution remotely sensed data to begin forecasting where species will move in space and time (Chong et al. 2001; Schnase et al. 2002). In addition, new leapfrog type dispersal models and theories of multiple invasions are needed that accommodate staggered entry points, many unused niches, under-used niches, lag-effects, greater potential coexistence, and the occasional highly dominant native species or super invaders in certain habitats (not all species are equivalents; Hubbell 2001). In light of the state- and county-level observations (Tables 1 and 3, Figures 1–3), future experiments and models should not assume that biodiversity is a barrier to invasion or that competition at small spatial scales translates to increased resistance to invasion at larger spatial scales (e.g., Naeem et al. 2000; Kennedy et al. 2002). Instead, ecologists must work across spatial scales to gain a better understanding of the covarying factors and processes that promote invasion in complex habitats, at larger scales than plant neighborhoods (Rejmánek 1989; Stohlgren 2002; Stohlgren et al. 2002, 2003).

Invasive species research will be hard pressed to keep pace with increased global trade and transportation systems, and the onslaught of invading plants, animals, and diseases. Natural selection may be accelerated, while changes in native species abundance and distributions may be subtle. We should probably target known super-invaders (e.g., selected pathogens and diseases, the brown treesnake, etc.), while keeping a watchful eye for the next voracious invaders.

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### Appendix A. Species richness and ancillary data used in this analysis.

Dataset	Description	Source
Native and non-indigenous plant species richness	Number of native and non-indigenous plant species per county	Biota of North America Program, John Kartesz, University of North Carolina Chapel Hill
Native and non-indigenous bird species richness	Number of native and non-indigenous bird species per county data	Bruce Peterjohn, US Geological Survey
Non-indigenous fish species richness	Number of non-indigenous fish species per 6-digit Hydrologic Unit Code (HUC)	Non-indigenous Aquatic Species Database, Pam Fuller, US Geological Survey
Native fish species richness	Number of native fish species per 6-digit Hydrologic Unit Code (HUC)	NatureServe, Larry Master, Chief Zoologist
Distance to coast	Distance from random point to coastline (km)	Derived, ArcView 3.2
Longitude, latitude	Location of random point, NAD 83	Derived, ArcView 3.2
Minimum temperature	Mean daily minimum temperature, Fahrenheit	National Climatic Data Center, Climate Maps of the United States database
Mean temperature	Mean daily average temperature, Fahrenheit	National Climatic Data Center, Climate Maps of the United States database
Precipitation	Mean total precipitation, inches	National Climatic Data Center, Climate Maps of the United States database
Crop acres	Number of acres in cropland per county in 1987	Environmental Research Systems Institute (ESRI, ArcView 3.2)
Human population	Number of people per county	Census 2000, US Census Bureau
Mean elevation <sup>a</sup>	Counties were defined as zones and zonal means of gridded elevation data were calculated. Measured in meters	Oregon Climate Service, PRISM digital elevation model (DEM), 1996
Variation in elevation <sup>a</sup>	Counties were defined as zones and zonal standard deviations of gridded elevation data were calculated	Oregon Climate Service, PRISM climate digital data, 1996
Potential evapotranspiration (PET) <sup>a</sup>	Thornthwaite's formula (Thornthwaite and Mather 1955)	Curtis Flather, USDA Forest Service
Vegetation carbon <sup>a</sup>	Total vegetation carbon (potential – no land use effects). Thirty year annual average (1961–1990) gC/m <sup>2</sup> at 3168 lat/lon locations, then gridded to county centroids	National Center for Atmospheric Research (NCAR). VEMAP2 DATA, 2000

## Appendix A. Continued.

Dataset	Description	Source
Road density <sup>a</sup>	Census Feature Class Codes A11 through A48 – primary highways with limited access through local neighborhoods, and rural roads. Measured in kilometers	Census TIGER/Line 1998 data, processed into state dbf files by USDA Forest Service, Geospatial Services and Technology Center (GSTC)
Habitat disturbance <sup>a</sup>	Index of habitat disturbance. Ratio of area of disturbed land (developed, herbaceous planted/cultivated, non-natural woody vegetation (e.g., orchards, vineyards), surface mines (e.g., quarries, strip mines, gravel pits) to total area in a county. Land cover classes as defined in the National Land Cover Data (NLCD)	National Land Cover Data (NLCD) developed from 30 m Landsat Thematic Mapper (TM) data by The Multi-resolution land Characterization (MRLC) Consortium, Version 09-06-2000
County area	Size of county (sq. km)	Environmental Systems Research Institute (ESRI), ArcView 3.2
HUC area	Hydrologic Unit Code Area (sq. km)	Environmental Systems Research Institute (ESRI), ArcView 3.2

<sup>a</sup>2003 Resource Interactions Database, John Hof, Curtis Flather, and Tony Baltic. USDA Forest Service, Rocky Mountain Research Station (Hof et al. in press).

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