Correlated non-native species richness of birds, mammals, herptiles and plants: scale effects of area, human population and native plants

Michael L. McKinney
Department of Earth & Planetary Sciences, University of Tennessee, Knoxville, TN 37996, USA
(e-mail: mmckinney@utk.edu)

Abstract

Several extrinsic factors (area, native species diversity, human population size and latitude) significantly influence the non-native species richness of plants, over several orders of magnitude. Using several data sets, I examine the role of these factors in non-native species richness of several animal groups: birds, mammals and herptiles (amphibians, reptiles). I also examine if non-native species richness is correlated among these groups. I find, in agreement with Sax [2001, Journal of Biogeography 28: 139–150], that latitude is inversely correlated with non-native species richness of many groups. Once latitude is accounted for, area, human population size and native plant species richness are shown to be important extrinsic factors influencing non-native animal species. Of these extrinsic factors, human population size and native plant species richness are the best predictors of non-native animal species richness. Area, human population size and native plant species richness are highly intercorrelated, along with non-native species richness of all taxa. Indeed a factor analysis shows that a single multivariate axis explains over half of the variation for all variables among the groups. One reason for this covariation is that humans tend to most densely occupy the most productive and diverse habitats where native plant species richness is very high. It is thus difficult to disentangle the effects of human population size and native species richness on non-native species richness. However, it seems likely that these two factors may combine to increase non-native species richness in a synergistic way: high native species richness reflects greater habitat variety available for non-native species, and dense human populations (that preferentially occupy areas rich in native species) increase non-native species importation and disturbance of local habitats.

Introduction

Pauchard and Shea (2006) discuss the importance of spatial scale in affecting dispersal and disturbance. As dispersal and disturbance are two key factors in determining the establishment of non-native species, it is clear that spatial scale will also influence non-native species establishment. Several lines of evidence indicate that spatial scale has a major influence on the species richness of non-native (and invasive) species. The exact nature of this influence varies among groups. For example, species richness of non-native freshwater fishes among US states is significantly positively correlated with state area, although this correlation does not hold for non-native plant species richness (McKinney 2001). Instead, non-native plant species richness is strongly correlated with native species richness across many spatial scales, ranging from small

parks to large US states (Levine and D'Antonio 1999; Lonsdale 1999; Stohlgren et al. 1999; McKinney 2001; Pysek et al. 2002). This correlation probably occurs because native plant species richness is a proxy variable that generally describes the area plus habitat diversity available for alien plant establishment (discussions in Levine and D'Antonio 1999; Lonsdale 1999).

Human population size is another important variable that often raises non-native species richness in plants (McKinney 2001). Human population is often, however, not independent of area or native species richness. Several studies show that human population tends to be higher in areas of high species diversity (Hunter and Yonzon 1993; Balmford et al. 2001; McKinney 2001; Araújo 2003; Chown et al. 2003). Another important variable affecting non-native species richness is latitude. For birds, mammals, fishes and plants, there is a tendency for non-native species richness to be very low in the tropics (Sax 2001). This is another covariable with native species richness, which tends to be very high in the tropics.

My goal in this paper is to use several data sets to examine the effects of these factors (area, native species diversity, human population size and latitude), on non-native species richness in several animal groups: birds, mammals and herptiles (amphibians, reptiles). In contrast to non-native plants, these factors have rarely been examined for their potential influence on non-native animals. I will also determine whether non-native species richness is correlated among these groups and whether some groups have generally higher proportions of non-native species. For example, do areas with many non-native bird species also tend to have many species of non-native mammals or reptiles? A correlation of groups among non-native species may arise because the two basic factors that promote the occurrence of non-native species in an area, rate of propagule introduction and survival rate of those propagules (Williamson 1996; Lonsdale 1999), have been documented as factors in the introduction of many taxa. For instance, highly modified urban core areas are dominated by non-native species of birds (Blair 2001), plants (Kowarik 1995), insects (McIntyre 2000) and mammals (Mackin-Rogalska et al.

1988). Conversely the same studies show that less urbanized areas of the gradient tend to be occupied by more native species for those same taxa.

On the other hand, there is also evidence that some of the factors promoting species introductions vary among taxa. For example, both human population size and native species richness are major factors in the United States that increase non-native plant species richness but they are not major factors increasing non-native fish species richness (McKinney 2001). Therefore, direct testing is needed to see if there is a correlation of non-native species richness between groups, and to assess the strength of that correlation.

Materials and methods

I assembled data on the number of non-native species of plants, herptiles (amphibians and reptiles), birds and mammals for 185 nations (including island nations), 50 US states and 23 protected areas. These data (the non-native species richness of each area) were regressed upon several variables to see if they had any explanatory influence. These explanatory variables included (for each area): native species richness, minimum and maximum latitude, human population size and area. However, as noted below, non-native species richness data were not available for some areas for some taxa. Minimum latitude is defined as the latitude occupied by the area (nation, state, protected area) that is closest to the equator while maximum latitude is the latitude occupied farthest from the equator.

Sources of data

In all cases, a non-native species is one that is recently introduced into the area (nation, state, protected area) from another nation by humans and has established a self-reproducing population. The number of native and non-native species for nations, US states and protected areas came from several sources. Bird species checklists were obtained from Avibase, the world bird database (http://www.bsc-eoc.org/avibase/avibase.jsp?, March 13, 2004.) These checklists provided
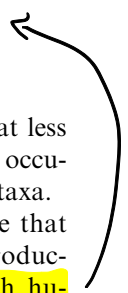
the number of non-native and native bird species per nation, and per state in the United States. I obtained checklists of non-native native and exotic plants, birds, mammals and herptiles (amphibians and reptiles) for protected areas, mostly national parks, in the USA from the database of ICE, Information Center for the Environment at the University of California, Davis (http://www.ice.ucdavis.edu/mab/index.html, March 22, 2004).

The number of non-native mammal species per nation came from from a checklist in Long's (2003) *Introduced Mammals of the World*. Number of non-native herptiles for several US states were obtained from a compilation in Butterfield et al. (1997). The number of native and non-native herptile and mammal species for several (but not all) US states was gotten through searches on the website of the Natural Heritage Network (http://www.natureserve.org, March 28, 2004). As discussed in McKinney (2001), the number of non-native plant species for US states came from Mac et al. (1998). This data set includes only plant species originating from outside of North America. The number of native plant species per state came from Stein et al. (2000). Numbers of non-native and native plant species in various nations were taken from the compilation by Vitousek et al. (1997).

As all of the data above on native and non-native plant, herptile, bird and mammal species originated from several sources, the results should be considered as preliminary and tentative. Obviously using different databases may introduce artifactual inconsistencies. To maximize consistency, non-native species for all taxa (plants, birds, mammals and herptiles) are defined as those that were imported into the nation, US state or protected area from another nation.

Data on human population, area, and maximum and minimum latitude for each nation came from *Factbook 2004* (http://www.cia.gov/cia/publications/factbook; January 13, 2004). The same data for US states came from the US Census Bureau (http://www.census.gov; January 15, 2004). For protected areas, only area and max/min latitude was used and these came from several published and cartographic sources describing these areas see McKinney (2002a).

Analysis

As noted, the non-native species richness of each area was regressed upon several variables to see if the variables had any explanatory influence. These explanatory variables included: native species richness, minimum and maximum latitude, human population size and area.

Statistical analysis of these data was carried out using SAS (1990). All of the variables, including human population, area, latitude, richness of native and non-native species per state, had frequency distributions that were strongly positively skewed. Therefore, the first step in the analysis was to transform the variables into an approximately normal distribution so that they could be compared with bivariate and multivariate regression methods without heteroscedastic biases. These variables were normalized by common logarithmic (base 10) transformation. A goodness of fit test (95% level of confidence) to a normal distribution was used to confirm that each transformed variable was successfully transformed to an approximately normal distribution.

I generated a correlation matrix to identify which variables were significantly correlated with one another. This was done to detect correlations between non-native species richness of the different taxa and factors influencing non-native species richness (such as human population, area, and latitude). Because the factors influencing non-native species richness were often correlated with one another, stepwise (forward) multiple regression was used to select the most important factors influencing non-native species richness. This regression method selects the most significant predictor variable and then the best predictor of the residual variance unexplained by the first predictor, and so on until no significant predictors remain (SAS 1990). This also calculated partial coefficients of determination (r^2) for each predictor, which estimates the percentage of variation explained by each predictor variable when the other predictor variables are held constant.

Another common method for analyzing covariant patterns is factor analysis. This multivariate method describes how much variation among all the variables can be explained by a single axis. A

418

second orthogonal axis is then created to determine how much residual covariation can be explained. Factor analysis was used here (SAS 1990), although it was used only for US states because it is very sensitive to missing data and the state data set was the most complete. Below I report the results of an orthomax rotation for the factor analysis, but other rotations (oblique, varimax) that were tried did not significantly alter the general pattern and results.

In addition to non-native species richness, I examined non-native species as a ratio with native species (i.e., non-native species richness/native species richness) for each group. I did this because there is a large difference among taxa in the number of non-native and native species richness. Dividing through (normalizing) by native species richness provides an approximate indicator whether taxa show similar patterns when these absolute differences are reduced.

Results

Maximum latitude was not significantly correlated with any variable. However, minimum latitude was significantly correlated with many variables, so all references to latitude below are to minimum latitude of the area (state, nation, park) analyzed. There is a significant correlation between the variables that influence non-native species richness (Table 1). For the entire data set (including nations, states and parks), area, human population and native plant species richness are all positively correlated. Area, human population, and native plant richness are all significantly inversely correlated with latitude. When nations below latitude 25° North are excluded, the same correlated patterns exist, except that the effects of latitude on area and human population are removed (Table 1).

Native plant species richness is consistently a very significant, and indeed often the best, predictor of non-native species richness of all four taxa (birds, mammals, herptiles and plants) for the entire data set and for locations above latitude 25° North (Table 2). Regression of non-native mammal and bird richness onto native plant richness illustrates the strong correlation (Figure 1). The regression parameters for this

are: Log(intmam) = 0.40 log(natplt) −0.50 and log(intbir) = 0.56 log(natplt) −1.08. In most cases, human population size and area are also consistently significant predictors of non-native species richness. However, population and area are generally less strongly correlated with non-native richness than is native plant richness (Table 2). Latitude is consistently correlated only with non-native herptiles, which has a significant negative correlation. A plot of native and non-native species for all taxa (with available data) shows that non-native species tend to show a classical species-area pattern (Figure 2).

Aside from native plant richness and area, another very consistent predictor of non-native species richness for each group is non-native species richness of the other groups. Non-native species richness is highly correlated among all groups for the entire data set and for locations above 25° North (Table 2). For example, regression of non-native mammals onto non-native birds (Figure 3) is highly significant, with the regression parameters: log(intmam) = 0.61 log(intbir) + 0.32.

Stepwise multiple regression showed that over half of the variation in non-native species richness could be explained in all four taxa: (For key to abbreviations, see Table 2).

Table 1. Correlation coefficients, significance, and sample size for log-transformed variables.

	Pop	Area	Natplt	Lat
All data				
Pop	1.000	0.654	0.630	−0.211
		< 0.0001	< 0.0001	0.0068
	163	163	70	163
Area	0.654	1.000	0.762	−0.308
	< 0.0001		< 0.0001	< 0.0001
	163	184	88	184
Natplt	0.630	0.762	1.000	−0.486
	< 0.0001	< 0.0001	< 0.0001	
	70	88	88	88
Lat > 25				
Pop	1.00000	0.52878	0.56406	−0.16332
		< 0.0001	< 0.0001	0.1178
	93	93	57	93
Area	0.52878	1.00000	0.76320	−0.06,335
	< 0.0001		< 0.0001	0.5031
	93	114	75	114
Natplt	0.56406	0.76320	1.00000	−0.39,220
	< 0.0001	< 0.0001		0.0005
	57	75	75	75

Natplt = native plants; lat = minimum latitude (see text).

Table 2. Correlation coefficients, significance, and sample size for log-transformed variables for all locations (top row for each taxon) and for locations above latitude 25° North (bottom row for each taxon).

intmam	**natplt**	natmam	**intherp**	**intplt**	**intbir**	**pop**	**area**	lat
	0.48	0.156	*0.657*	0.377	0.466	0.285	0.301	−0.073
	0.001	0.172	<0.0001	0.0064	<0.0001	0.0258	0.0059	0.5067
	51	78	37	51	80	61	82	83
intmam	**natplt**	natmam	**intherp**	**intplt**	**intbir**	**pop**	**area**	lat
	0.38	0.135	*0.657*	0.324	0.43	0.532	0.298	−0.078
	0.007	0.2817	<0.0001	0.0229	<0.0001	<0.0001	0.0127	0.5172
	49	65	37	49	68	48	69	70
intbir	**natplt**	natbir	**intherp**	**intplt**	**intmam**	pop	area	**lat**
	0.61	−0.059	0.548	*0.697*	0.455	0.041	0.048	0.352
	<0.0001	0.4260	0.0001	<0.0001	<0.0001	0.6021	0.5182	<0.0001
	85	179	43	86	80	157	178	179
intbir	**natplt**	**natbir**	**intherp**	**intplt**	**intmam**	pop	**area**	lat
	0.60	0.402	0.548	*0.690*	0.429	0.079	0.243	−0.114
	<0.0001	<0.0001	0.0001	<0.0001	0.0003	0.4541	0.0097	0.2271
	74	113	43	75	68	91	112	113
intherp	**natplt**	**natherp**	**intmam**	**intplt**	**intbir**	**pop**	**area**	**lat**
	0.61	*0.756*	0.657	0.541	0.548	0.426	0.502	−0.623
	<0.0001	<0.0001	<0.0001	0.0004	0.0001	0.0423	0.0007	<0.0001
	39	38	37	39	43	23	42	43
intherp	**natplt**	**natherp**	**intmam**	**intplt**	**intbir**	**pop**	**area**	**lat**
	0.61	*0.756*	0.657	0.541	0.548	0.426	0.502	−0.623
	<0.0001	<0.0001	<0.0001	0.0004	0.0001	0.0423	0.0007	<0.0001
	39	38	37	39	43	23	42	43
intplt	**natplt**	**intmam**	**intherp**	**intbir**	−	**pop**	**area**	lat
	0.688	0.377	0.541	0.687	−	0.485	0.526	−0.027
	<0.0001	0.0064	0.0004	<0.0001	−	<0.0001	<0.0001	0.7990
	87	51	39	80	−	70	88	88
intplt	**natplt**	**intmam**	**intherp**	**intbir**	−	**pop**	**area**	lat
	0.788	0.324	0.541	0.690	−	0.611	0.562	−0.144
	<0.0001	0.0229	0.0004	<0.0001	−	<0.0001	<0.0001	0.2116
	75	49	39	75	−	58	76	76

Abbreviations: int = non-native, nat = native. *Example*: intmam = non-native mammals; natplt = native plants; pop = human population, lat = minimum latitude (see text).

$$\text{Intplt} = 0.83\,\text{intbir} + 0.21\text{pop} + 4.71; n = 67$$
$$(r^2) \qquad (0.51) \qquad (0.08)$$

$$\text{Intbird} = 0.26\text{intplt} + 0.36\text{intmam} - 0.35; n = 67$$
$$(r^2) \qquad (0.51) \qquad (0.12)$$

$$\text{Intmam} = 0.29\text{intherp} + 0.31\text{natmam}; n = 34$$
$$(r^2) \qquad (0.43) \qquad (0.09)$$

$$\text{Intherp} = 0.35\text{natherp} + 0.73\text{intmam} + 0.59\text{intbir} - 1.51\text{lat}; n = 32.$$
$$(r^2) \qquad (0.59) \qquad (0.12) \qquad (0.05) \qquad (0.04)$$

The factor analysis of the US state data revealed two axes that were significant (Table 3). The first axis of covariation accounted for over half (54%) of the variance among seven variables (human population, area, native plant richness, and non-native richness of mammals, herptiles, plants and birds). In contrast, latitude had a strong negative correlation with this axis (negative loading). The second axis is also significant, explaining 24% of the total variation. The
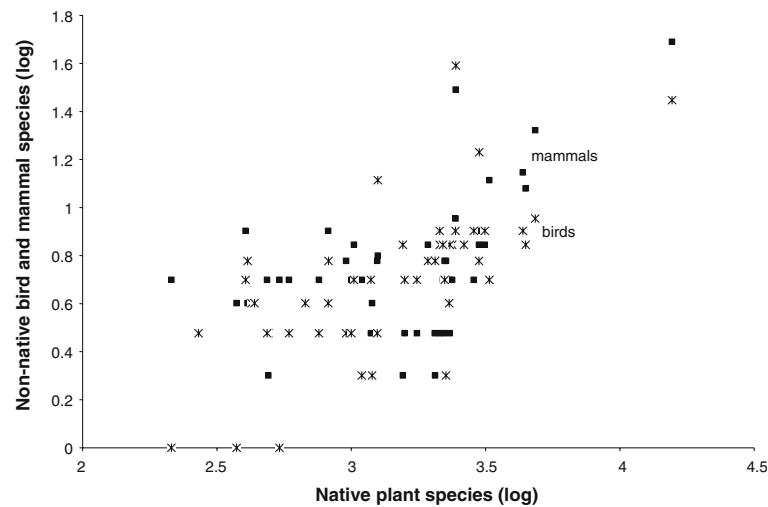
Figure 1. Correlation between native plant species-richness and richness of non-native birds and mammals. Mammals = black squares; birds = asterisks.
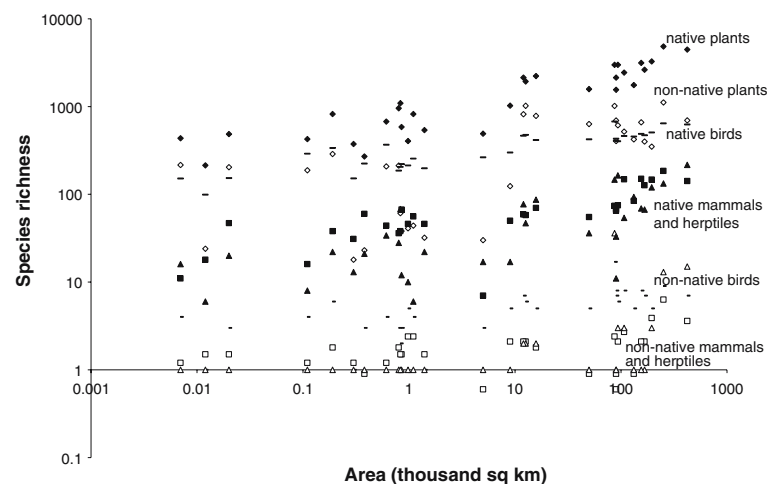

Figure 2. Log–log species-area pattern for native and non-native species for nations, US states, and protected areas. $N = 34$ for all point clouds. Only those areas with data available for all taxa are shown. Native plants = black diamonds; non-native plants = open diamonds; native birds = large dashes; non-native birds = small dashes, black squares = native mammals; open squares = non-native mammals; black triangles = native herptiles; open triangles = non-native herptiles.

loadings on the second axis for non-native species richness of all taxa were positive. In contrast, the remaining (after latitude was removed) extrinsic variables that influence non-native richness (area, native plant richness and human population size) were negative (Figure 4).

When all three animal groups are compared to plants in terms of proportion of species non-native (non-native species richness/native species richness), only proportion of non-native bird species shows a significant correlation with non-native plants ($r = 0.51$; sig. > 0.01; $n = 85$). The proportion of birds is much smaller than plants, being far below the line of isometry (Figure 5). While they do not correlate strongly with plants, both mammals and especially herptiles also generally
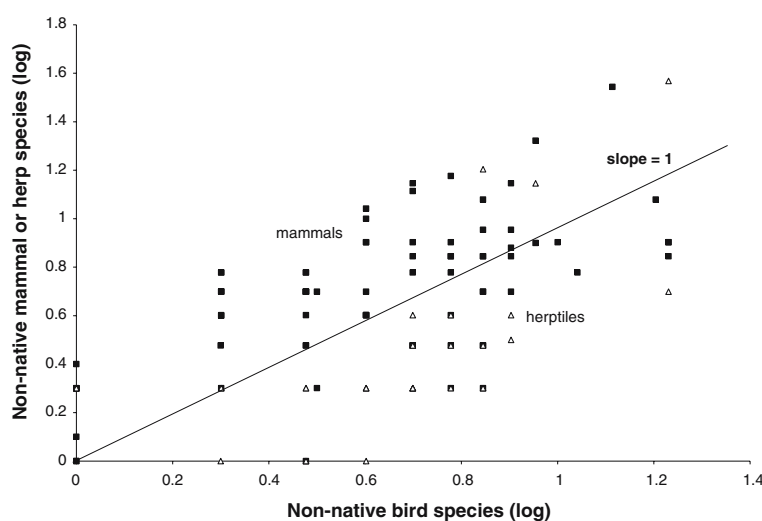
Figure 3. Correlation between non-native bird species richness and richness of non-native mammals and herptile species. Mammals = black squares; herptiles = open triangles.

Table 3. Factor analysis results. These are the loadings for each variable.

	Factor 1	Factor 2
pop	0.80912	−0.31984
area	0.44737	−0.79403
natplt	0.88783	−0.30935
lat	−0.75165	0.06512
intplt	0.55812	0.76759
intbir	0.65590	0.29094
intmam	0.80035	0.12861
intherp	0.87025	0.16213
Proportion variance explained	54.35	24.26

For variable abbreviations, see Table 2.

have a lower proportion of species non-native, although not as low as birds (Figure 5).

Discussion

That latitude is inversely correlated with non-native species richness provides independent support for Sax (2001) who found this same pattern (outside the tropics) in several taxa, with completely different data sets. Sax (2001) suggests that this pattern occurs because non-native species must adapt to the same set of physical and biotic conditions as native species, which also

tend to decline in species-richness with increasing latitude.

Once latitude is accounted for, area, human population size and native plant species richness are shown to be important extrinsic factors influencing non-native species. These three variables are highly intercorrelated, along with non-native species richness of all taxa so all load highly on the first axis of the factor analysis. It seems likely that area is the more basic of the three extrinsic factors influencing non-native species. This is because native species richness is ultimately a function of area, as described by species-area patterns common in native plants (Rosenzweig 1995). Similarly, human population size also tends to increase with area.

Given the importance of species-area patterns to ecology, it is interesting to consider the causes of species-area patterns for non-native species. Explanations for the pattern in native species focus on sampling plus the mechanistic causes of evolution, dispersal and habitat diversity (Rosenzweig 1995). Assuming that evolution does not play a role in non-natives due to their recent introduction, it would seem that sampling, dispersal, and habitat variety are factors producing the species-area curve in non-native species. For example, habitat diversity available for non-natives increases with area including habitat created by anthropogenic
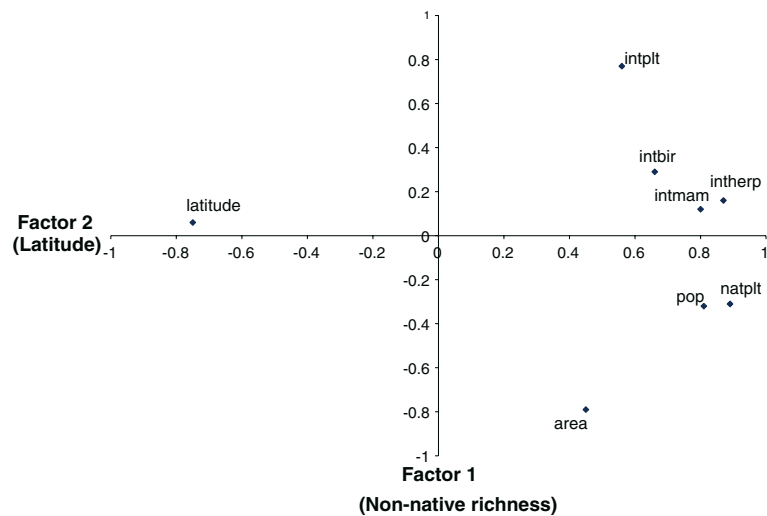
Figure 4. Plot of factors 1 vs. 2 of the factor analysis. See text for discussion. Abbreviations explained in Table 2.
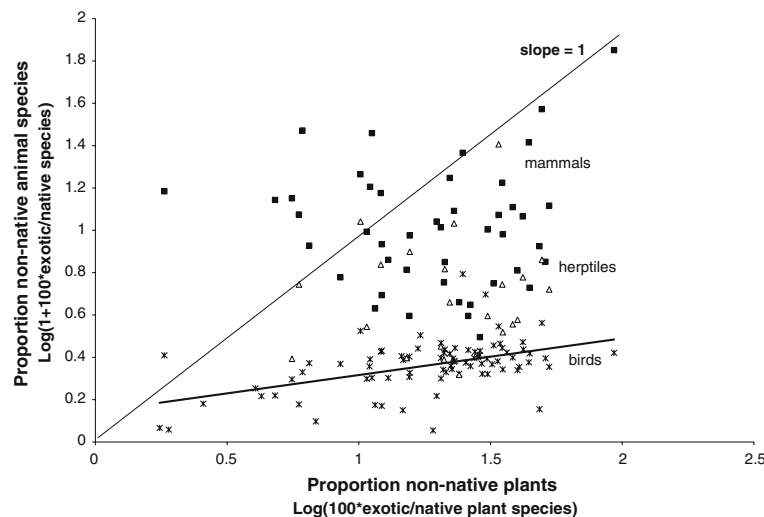

Figure 5. Proportion of non-native plants is strongly correlated with proportion of non-native birds, although birds have a much lower proportion as shown by the line of isometry. Birds = asterisks, mammals = black squares, herptiles = open triangles. Herptiles and especially mammals have much greater proportions of non-native species relative to birds.

disturbances, which is scale-dependent (Pauchard and Shea, 2006).

It is also notable that the rank order of the species-area curves are similar for non-natives. In other words, the curve for non-native plants has the highest *y*-intercept among non-native taxa, just as native plants have the highest *y*-intercept among native taxa (Figure 2). Similarly, non-native birds are next-highest, with non-native mammals and herptiles having the lowest *y*-intercept.

This follows the same order as native species in those taxa, where mammals and herptiles have the lowest *y*-intercepts. Again, this indicates a parallel with native species: native plants have a smaller average and minimum geographic range size than mammals and birds (Gaston et al. 1998). This is likely true for non-native species. It is, therefore, possible to have higher species richness of non-native plants per unit area of plants than mammals or and birds.

However, compared to area, human population size and native plant species richness are better predictors of non-native animal species richness. That human population size is a main predictor of non-native species richness was shown by McKinney (2001), but only for US state plant introductions. Chown et al. (1998) showed that human population is an important predictor of mammal and insect species richness, but their study focused on islands. My findings here are the first, to my knowledge, documenting that human population size is a significant factor increasing species richness of non-native mammals and herptiles on continents. The reason for this correlation are probably more complex than it first appears. Human population size will be related to importation rate of new species, as well as rate of land use transformation, i.e., disturbances which tend to create habitat for non-native species (McKinney 2002b). It is interesting that non-native bird species richness does not correlate with human population size. Perhaps this is because, as with non-native fishes in the US, many introductions are driven by game agency and other releases for sport. However, this is only speculation and needs further testing.

Native plant species richness is an even stronger and more consistent predictor of non-native species richness, being found for all four groups. This correlation has been reported before, but only for plants (Levine and D'Antonio 1999; Lonsdale 1999; McKinney 2001; Pysek et al. 2002). It has been suggested that this correlation occurs because native species richness tends to correlate with area plus the habitat diversity available for non-native species to colonize (Levine and D'Antonio 1999; Lonsdale 1999).

My results extend this native plant correlation from non-native plants to non-native animal species richness. One explanation is that, as with non-native plants, native plant richness is a proxy variable that approximates the amount of area plus habitat diversity for non-native birds, mammals and herptiles to colonize. However, this explanation is probably incomplete because there is also a strong correlation between native plant richness and human population size. In addition to this study, a native species richness-human population association has been reported in other studies, at several spatial scales and for

several taxa (plants, mammals, birds) of native species (Hunter and Yonzon 1993; Balmford et al. 2001; McKinney 2001; Araújo 2003; Chown et al. 2003). The reason for this association seems to be that humans tend to most densely occupy the most productive and diverse habitats because they are most conducive to human population growth (Balmford et al. 2001; Araújo 2003).

Because of their strong statistical association, it is very difficult to disentangle the effects of human population size and native species richness on non-native species richness. However, it seems likely that these two factors may combine to increase non-native species richness in a synergistic way, with native species richness providing greater potential habitat variety and humans creating propagule pressure as well as creating habitat. Further testing will be needed to assess the relative effects of these two variables on different taxa and in different situations.

Aside from the extrinsic variables (area, human population, and native species richness), there is also a strong statistical association among number of non-native species among the different taxa. This is shown the second axis on the factor analysis. As this occurs after the extrinsic variables are accounted for on the first axis, this association implies that it may be caused by yet another extrinsic variable (or set of variables) besides area, human population and native species richness. I suggest that a human activity factor, that measures *per-capita* human impact, would be a likely candidate to account for much of this residual variation. Aside from the number of humans in an area, a very important factor affecting non-native species richness would be how those humans are living. A million people concentrated in a highly urbanized area would probably have a different impact on new species introductions than a million people practicing traditional farming, for example.

When relative non-native species richness is examined (non-native richness/native richness), there is still a correlation between non-native plants and birds. However, non-native birds consistently show a much lower proportion than non-native plants in the areas where they co-occur. Non-native mammals and herptiles also tend to show lower proportions than plants, although

these are typically higher than relative bird introductions. Explaining these patterns will require data on relative introduction rate and study of the factors promoting non-native establishment among the taxa. However, it seems likely that the smaller geographic range size of plants compared to vertebrates (Gaston et al. 1998), would play a role.

In conclusion, these results show that non-native species richness is influenced by several factors that are related to spatial scaling. The most direct spatial factor is area, whereby non-native species show a species-area effect that is similar to that of native species, although the y-intercept of the curve is lower in non-natives. The underlying causal mechanisms of this curve include the spatial scaling of disturbance (which creates habitat for non-natives) and limits to dispersal (Pauchard and Shea, this issue). However, this species-area effect is confounded by a synergism with human population and native plant species richness which also increase with area, and are also factors that (independent of area) increase non-native animal species richness.

My findings complement the study by Stohlgen and others (2006) who also find that non-native species richness of several taxa are intercorrelated with each other as well as with human population and abiotic factors. In addition to the patterns found in their study of plants, birds and fishes (Stohlgren et al. 2006), I show that similar patterns are also apparently found in mammals, reptiles and amphibians.

References

Araújo MB (2003) The coincidence of people and biodiversity in Europe. Global Ecology & Biogeography 12: 5–12

Balmford A, Moore JL, Brooks T, Burgess N, Hansen LA, Williams P and Rahbek C (2001) Conservation conflicts across Africa. Science 291: 2616–2619

Blair RB (2001) Birds and butterflies along urban gradients in two ecoregions of the United States. In: Lockwood JL and McKinney ML (eds) Biotic Homogenization, pp 33–56. Kluwer, New York

Butterfield BP, Meshaka WE and Guyer C (1997) Non-indigenous amphibians and reptiles. In: Simberloff D, Schmitz DC and Brown TC (eds) Strangers in Paradise, pp 123–138. Island Press, Washington, DC

Chown SL, Gremmen NJM and Gaston KJ (1998) Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts, and conservation. American Naturalist 152: 562–575

Chown SL, van Rensburg BJ, Gaston KJ, Rodrigues ASL and van Jaarsveld AS (2003) Species richness, human population size and energy: conservation implications at a national scale. Ecological Applications 13: 1233–1241

Gaston KJ, Quinn RM, Blackburn TM and Eversham BC (1998) Species-range distributions in Britain. Ecography 21: 361–370

Hunter ML and Yonzon P (1993) Altitudinal distributions of birds, mammals, people, forests, and parks in Nepal. Conservation Biology 7: 420–423

Kowarik I (1995) On the role of alien species in urban flora and vegetation. In: Pysek P, Prach K, Rejmanek M and Wade M (eds) Plant Invasions – General Aspects and Special Problems, pp 85–103. SPB Academic Publishing, Amsterdam

Levine JM and D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15–26

Long JL (2003) Introduced Mammals of the World. Wallingford, CABI, Collingwood, Victoria, Australia,

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522–1536

McIntyre NE (2000) Ecology of urban arthropods: a review and a call to action. Annals of the Entomological Society of America 93: 825–835

McKinney ML (2001) Effects of human population, area and time on non-native plant and fish diversity of the US. Biological Conservation 100: 243–252

McKinney ML (2002a) Influence of settlement time, human population, park shape and age, visitation and roads on the number of alien plant species in protected area in the USA. Diversity & Distributions 8: 311–318

McKinney ML (2002b) Urbanization, biodiversity and conservation. BioScience 52: 883–890

Mac MJ, Opler PA, Haecker CE and Doran PD (1998) Status and Trends of the Nation's Biological Resources, Vol 1, US Geological Survey, Reston, Virginia

Mackin-Rogalska R, Pinowski J, Solon J and Wojcik Z (1988) Changes in vegetation, avifauna, and small mammals in a suburban habitat. Polish Ecological Studies 14: 293–330

Pauchard A and Shea K (2006) Integrating the study of alien plant invasions across spatial scales. Biological Invasions 8: 415–429

Pysek P, Jarosik V and Kucera T (2002) Patterns of invasion in temperate nature reserves. Biological Conservation 104: 13–24

Rosenzweig ML (1995) Species Diversity in Space and Time. Cambridge University Press, Cambridge UK

SAS (Statistical Analysis Software) (1990) SAS User's Guide. SAS Institute, Cary, North Carolina

Sax DF (2001) Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. Journal of Biogeography 28: 139–150

Stein BA, Kutner L and Adams J (2000) Precious Heritage. Oxford University Press, Oxford, UK

Stohlgren TJ, Barnett D, Flather C, Fuller P, Peterjohn B, Kartesz J and Master LL (2006) Species richness and

patterns of invasion in plants, birds, and fishes in the United States. Biological Invasions 8: 443–463

Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Bashkin M and Son Y (1999) Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25–46

Vitousek PM, D'Antonio CM, Loope LL, Rejmanek M and Westbrooks R (1997) Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21: 1–16

Williamson M (1996) Biological Invasions. Chapman & Hall, London