PATTERNS OF PLANT SPECIES RICHNESS IN THE CONTIGUOUS UNITED STATES

Erika Y. Chin
Department of Geography
State University of New York at Binghamton
Binghamton, NY 13902

ABSTRACT: *Spatial distribution patterns of native and exotic species have frequently been studied to find general processes behind species distribution and invasion, but thus far no consensus has been reached. Two biogeographic patterns often used in such studies are the latitudinal gradient, which describes declining biodiversity with increasing latitude, and the species-area relationship, describing the positive relationship between species richness and habitat area. Large scale studies of North American plant diversity using county-level data have provided conflicting results, fueling ongoing debates on plant distribution patterns in the US. A potential cause of these inconsistencies may be incomplete floristic records, resulting in underestimates of species richness. Therefore, analysis of floristic records at the county level may be an inadequate scale to firmly establish latitudinal and species area relationships. Adjacent counties within the same state are likely to have similar species present, so using state-level floristic records would likely reduce bias arising from incomplete surveys. This study examined US native and introduced plant distributions to determine general patterns of species diversity relationships at smaller spatial scales. A slight latitudinal gradient of native species richness was observed, with more states in the southern US having higher native species richness. Coastal states also had higher native richness, with the exception of Texas and New England states. States with high introduced species richness showed no clear latitudinal gradient. Highest introduced richness was in California, New York, and Florida. Given these results introduced species do not appear to follow the species-area relationship or latitudinal gradient.*

Keywords: *distribution patterns, species richness, species-area curves, introduced plants*

INTRODUCTION

Species introduction and invasion are well studied topics in biogeography and ecology. Much research on introduced species has focused on finding specific biological traits that allow a species to become a successful invader (Blumler 2006). The desire to develop ecological invasion rules may bias researchers towards downplaying the importance of geographic factors, or accepting ecological explanations with little consideration to potential geographic effects (Blumler 2006). Species introduction is both an ecological and spatial issue, and geographical considerations should be taken into account in order to fully understand the causes and effects.

The movement of individual organisms away from existing populations is a common biological event that has major implications for species evolution and ecosystem dynamics. As plant species have limited mobility they often rely on seed dispersal and the spread of new propagules to expand their ranges. However, such dispersal is naturally limited by geographic and environmental barriers such as oceans and varying climates along mountain ranges. With globalization and increased international trade and travel, the number of human mediated dispersal events has greatly increased (Thuiller et al. 2005).

The introduction of plant species to new environments is particularly dependent on human activity. Seeds are often scattered along trails and roads after being unintentionally carried by humans, or dispersed by roadside mowing and landscaping (Mabry 2003, Mortensen et al. 2009). Besides acting as corridors for invasive species movement, Mortensen et al. (2009) demonstrated that forest roads can be ideal locations for initial population establishment. Increased land development (e.g. paved roads as opposed to trails or dirt roads) was also found to positively correlate with the abundance of several invasive plant species in New England (Lundgren et al. 2004).

In the attempt to identify the spatial patterns behind exotic species invasion, native and introduced species distributions have been widely studied across varied spatial scales. Studies have attempted to relate species distribution patterns to human disturbances and other biogeographic factors, but this has resulted in conflicting hypotheses rather than unifying distribution theories. The latitudinal diversity gradient is one widely recognized biogeographic pattern used in such studies, which describes the increase in species richness moving from the poles to equatorial regions (Hillebrand 2004). Previous studies have investigated native plant species richness along a latitudinal gradient (e.g. Glenn-Lewin 1977, Stevens 1989, Rosenzweig 1995, Qian 1999), but a general consensus on the underlying processes has yet to be reached (Hillebrand 2004). Other studies have compared distribution patterns of native and introduced plant species in North America (Qian et al. 2007, Fridley 2008, Denslow et al. 2010), but few have looked at distribution in relation to the latitudinal diversity gradient. These studies have also obtained conflicting results, largely due to inherent limitations in using floristic records (Fridley et al. 2006, Jarnevich et al. 2006). An analysis conducted by Stohlgren et al. (2005) of native and non-native plant species in the coterminous US found no relationship between native plant richness and latitude, contrary to its well documented occurrence worldwide (Qian 1999, Hillebrand 2004). Fridley et al. (2006) attributed this finding to the use of incomplete species richness data at the county level. As any size area is unlikely to have a fully complete floristic inventory due to the inherent difficulties of sampling and managing floras (Flather et al. 2006), this is likely a major factor in such inconsistencies between studies.

Related studies have used species occurrence data from the Biota of North America Program (BONAP), which many regard as the "the standard plant data set for many government and nongovernment agencies" (Stohlgen et al. 2005). However, studies by Stohlgren et al. (2005) and Fridley et al. (2006) using county-level data from this source observed contradictory trends in native plant species richness and latitude. Given the discrepancies naturally found in floristic data, and that species lists in many counties are not created with the intention of recording a comprehensive record of species present (Palmer 1995), analysis of species richness at the county level is likely to produce outliers and skew statistical results.

Coterminous and neighboring counties in the same state, however, are likely to have more similar species present than counties in distant states found at different latitudes (Tobler 1970, Hillebrand 2004, Qian et al. 2007). Using state-level floristic records would provide a more complete record of present species for statistical analysis while still displaying spatial patterns of species distribution. This study also used data from the USDA PLANTS database in order to assess how consistent species distribution patterns would be using an alternative dataset.

Examining state-level plant species distribution patterns compliments studies of native and introduced plant richness done at larger spatial scales. The objectives of this study were to determine general patterns of plant diversity in the contiguous US and to compare diversity relationships between native and introduced plant species. The use of an alternative floristic dataset from previous studies also served to test assumed species diversity relationships, in which (1) larger states will contain more species (the species-area relationship), and (2) more southern states will have higher species richness values (the latitudinal diversity gradient). Spatial distributions of native and introduced plant species in relation to latitude and human disturbances were also tested in the expectation that human impacts would more strongly influence introduced species diversity than latitudinal or area relationships.

METHODS

The 48 contiguous United States as a whole were studied, and then subdivided into "Western" and "Eastern" state groups for more detailed analysis. Western states ranged from ND south to TX and west to the coast, while Eastern states included those from MN to LA and east. This was done so that the environments within each grouping are more similar to each other, reducing the potential number of different biomes and habitats within each area. Since large geographic areas have been shown to accommodate higher biodiversity in part due to ecosystem variation (Rosensweig 1995, MacArthur and Wilson 1967), this grouping system reduces the effect of habitat variation on species richness. Differences in introduction patterns between the Eastern and Western US would also be more apparent.

Data from the United States Department of Agriculture PLANTS Database were downloaded in May 2011. This database includes information on all plant species reported to be present in the United States, including state occurrence and native status. The total number of plant species present in each state was counted to obtain state species richness values. Species were classified as either being native to the US (naturally occurring in North America) or introduced (non-native species having natural habitats found outside of North America). The degree of association between each state's species richness value and latitude and longitude (using the geographic centroids), state population density, and year of first permanent European settlement was evaluated. State population and geographic data were obtained from the 2010 US Census, and year of first permanent settlement was obtained from each state's official government website.

Testing species richness against latitude measured the effect of the latitudinal diversity gradient. As the location of a species' initial introduction can influence the spread and location of its local populations (Blumler

2006), the relationship between introduced species richness and state longitude was also examined to reveal if a pattern of species introductions along the coasts exists. In states with higher population densities and longer periods of European settlement human disturbances are likely to be greater (Stohlgren et al. 2005), so state population density and year of first European settlement was used as a proxy to gauge relative disturbance levels in each state. Log-transformed native and introduced species counts within the CONUS and Western US groups did not follow a normal distribution after performing the Shapiro-Wilk test for normality, so the non-parametric test Spearman's rank correlation coefficient was used in all data analyses. All statistical analyses were done using SPSS.

Species-area curves were constructed for native and introduced plant species in the US to evaluate species-area relationships. Species-area curves were created using the semilog model $\log_{10}S = \log_{10}C + z \log_{10} A$, where S = number of species per state, A = state area, and C and Z are constants calculated from the dataset. Six separate curves were graphed: Contiguous US (CONUS) Native Species, CONUS Introduced Species, Eastern US (EUS) Native Species, EUS Introduced Species, Western US (WUS) Native Species, and WUS Introduced Species. States were categorized based on position above or below the fitted species area curve. States above the curve have relatively higher species richness than states found below the curve. States were further divided based on the quartile of their log-transformed species count to differentiate between states with "high" species richness (≥ Quartile 3) or "low" species richness (< Quartile 1). Linear regressions were performed on all curves to evaluate the degree of association between state area and number of species using Spearman's rho. Results were mapped using ArcGIS 10.

RESULTS AND DISCUSSION

The Species-area Relationship and Latitudinal Gradient

In all three state groupings (CONUS, EUS and WUS) as state area increased the number of native species in each state increased. Spearman's rho between native species richness and state area was statistically significant in all three curves (see Table 1), indicative of MacArthur and Wilson's (1967) species area effect. There was a slightly negative relationship between state area and introduced species in CONUS (see Figure 1 and Table 2), contrary to the expected species-area relationship. Correlation in Western and Eastern introduced species-area curves were not statistically significant. This result suggests that factors other than state area have a greater influence on the distribution of introduced species.

Table 1. Spearman's Rho Correlation Coefficients Between Native Species Richness

Native Species Richness	CONUS (N = 48)	WUS (N = 17)	EUS (N = 31)
state area	0.553**	0.706**	0.479**
state population density	-0.078	0.593*	0.110
year state settled	0.085	-0.442	-0.080
state latitude	-0.484**	-0.576*	-0.721**
state longitude	-0.491**	-0.525*	-0.321

** P< 0.05, ** P < 0.01*

Table 2. Spearman's Rho Correlation Coefficients for Introduced Species Richness

Introduced Species Richness	CONUS (N = 48)	WUS (N = 17)	EUS (N = 31)
state area	-0.403**	0.377	-0.062
state population density	0.765**	0.598*	0.612**
year state settled	-0.604**	-0.317	-0.499**
state latitude	-0.139	-0.159	-0.086
state longitude	0.474**	-0.463	0.370*

** P< 0.05, ** P < 0.01*

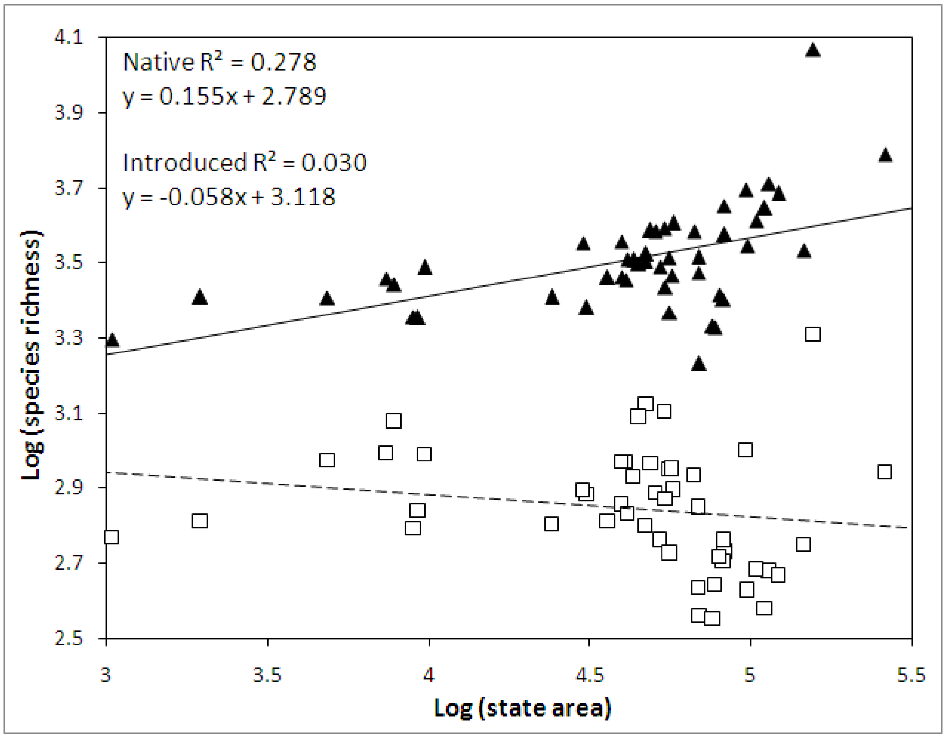

Figure 1. Native and introduced species-area curves for the contiguous US. State native species richness values are represented by filled in triangles, and the solid line is the linear least squares regression calculated from native species and state area. Introduced species are represented by open squares with a dashed regression line.

Native species richness was moderately correlated with state latitude (see Table 1), indicating that more native species are found in Southern states (see Figures 3, 5, 6). However, there was no significant correlation between introduced species and latitude (Figures 4, 5, 6). States with highest introduced species richness are California, New York, and Florida. Introduced species do not follow any latitudinal gradient at the state level.

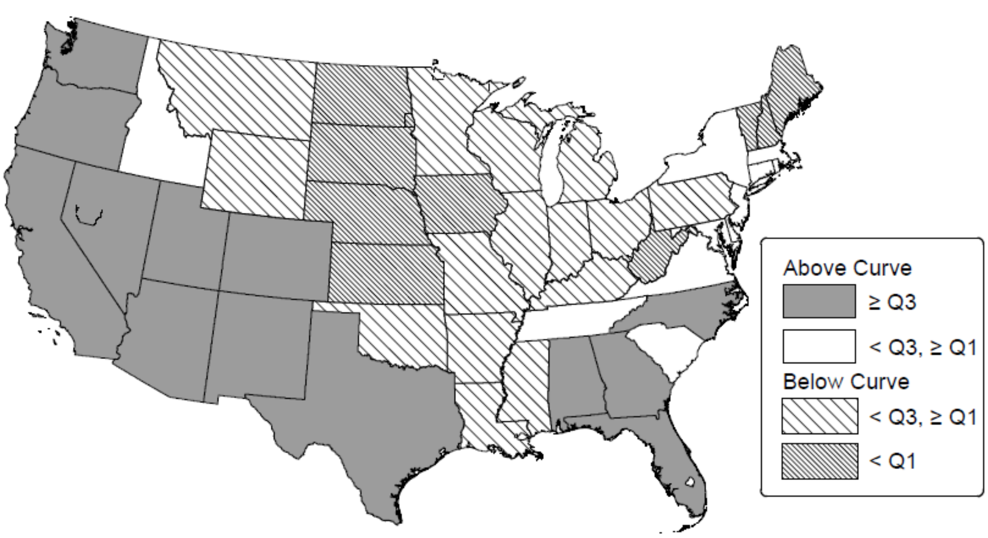

Figure 3. State quartile rankings of native species richness values in the contiguous United States.

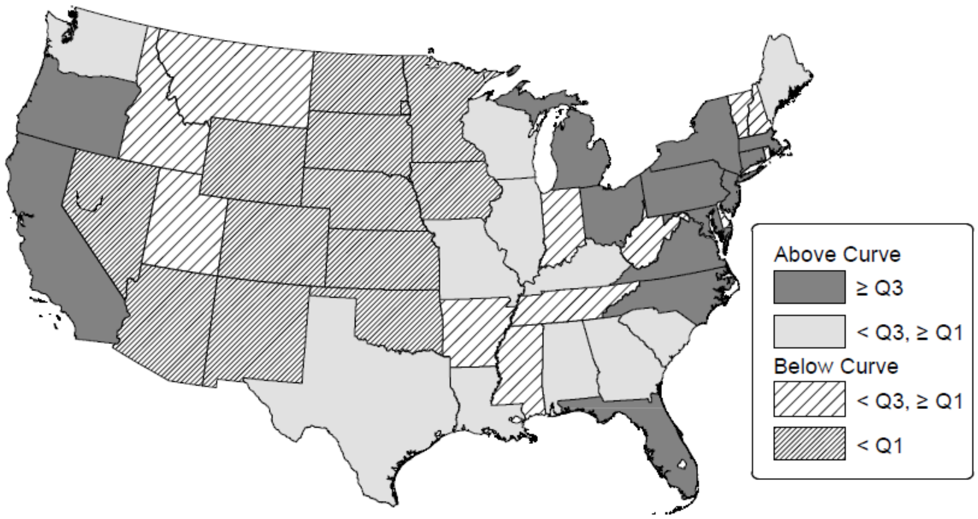

Figure 4. State quartile rankings of introduced species richness values in the contiguous United States.

Results from this study using the PLANTS dataset corresponded with those from Fridley et al. (2006), where a significant relationship was observed between native species richness and latitude. Based on these results, it appears that the contrasting observation made by Stohlgren et al. (2005) were due to differences in their interpretation of the dataset. In introduced species, the species-area relationship and latitudinal diversity gradient are not observed at the state scale.

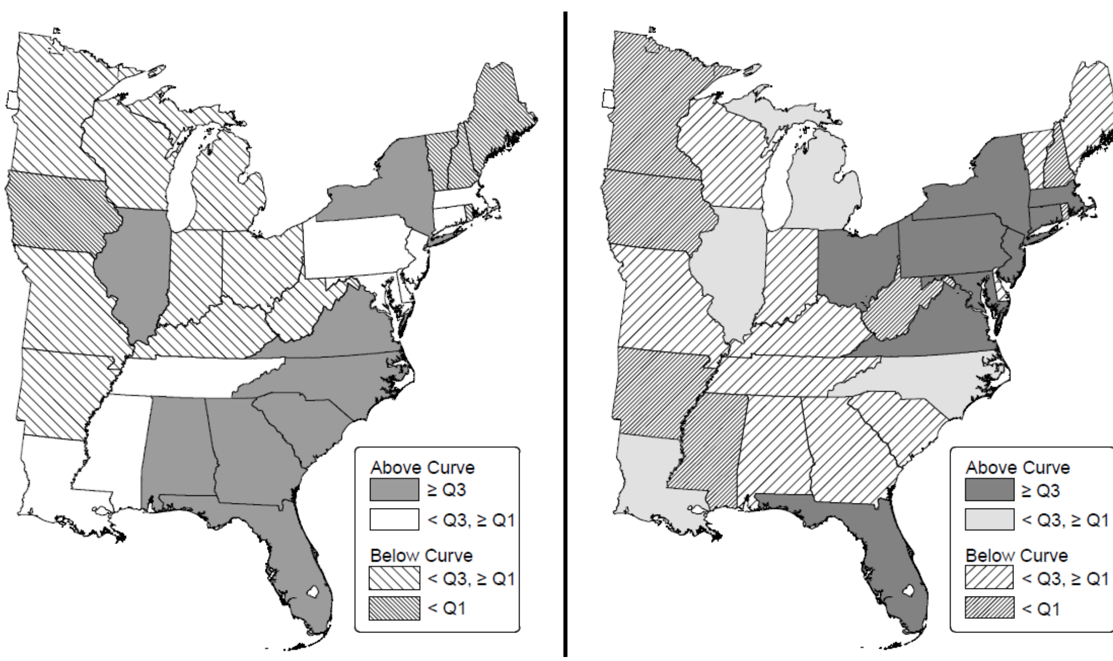

Figure 5. Eastern US native (left) and introduced (right) quartile rankings of species richness values.

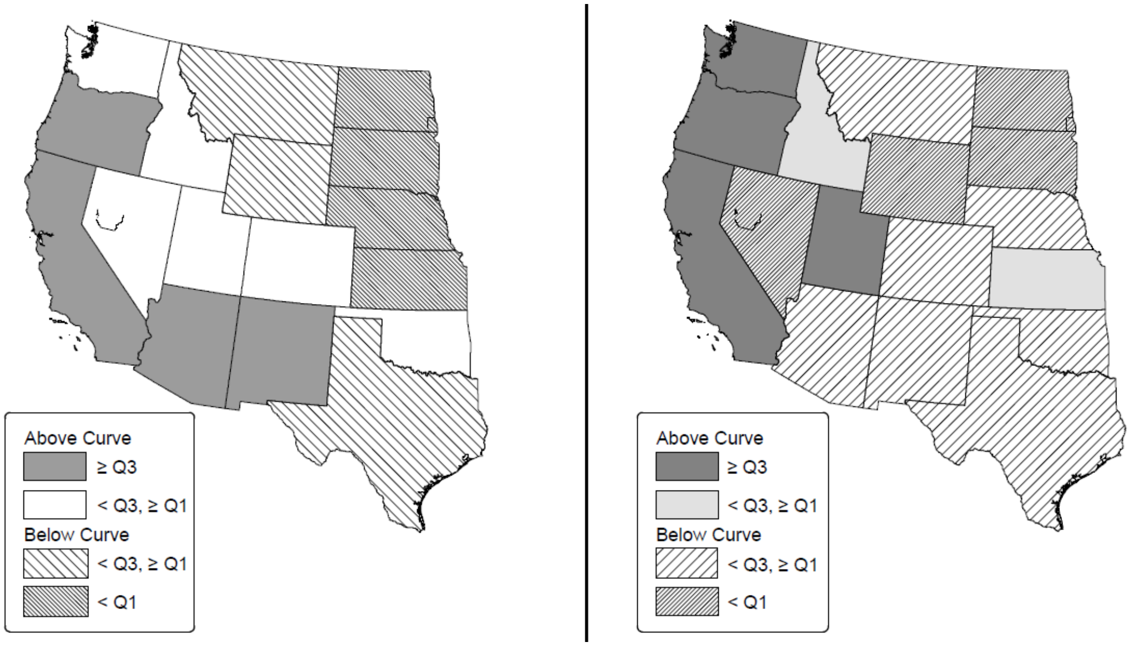

Figure 6. Western US native (left) and introduced (right) quartile rankings of species richness values.

Human Activity and Introduced Species

Introduced species richness was tested for correlation with state longitude, year of first European settlement, and state population. At the level of the contiguous US, introduced species richness was significantly correlated with state longitude, state population, and year of settlement (see Table 2). Results were similar at the Eastern and Western US groupings, but the strength of the correlations were not as high.

Native species followed the expected patterns of the species-area relationship and latitudinal diversity gradient, but this was not true of introduced species. The negative correlation between introduced species and state area indicates that factors independent of latitude are influencing introduced species distributions. Across CONUS there is no significant correlation between native and introduced species richness values (r = 0.205, p = 0.163), confirming that a difference between native and introduced species distributions exists. One possible cause of the negative introduced species-area curve is that introduced species are not in equilibrium with their environment. As introduced species are still in the process of invasion they have not all established stable populations, unlike most native species. This is most apparent in the larger states, where there is a much greater area that introduced species can potentially invade, but have yet to do so.

Variables measuring human influences had stronger correlations than other factors tested. Introduced species were the most closely correlated with state population, in comparison with the other variables. While introduced species did not follow a latitudinal diversity gradient, there was moderate correlation between introduced species and longitude, demonstrating that more introduced species were found along the East and West coasts (see Figures 3-6). This is consistent with human settlement patterns, where most people initially established settlements along the coasts before moving inland. More introduced species are also found in states with older settlements, many of which are found along the Eastern Seaboard. However, the pattern of higher species richness along the coast is also observed in native species, and there is moderate correlation between native and introduced species in EUS (r = 0.466, $p < 0.01$) and WUS (r = 0.642, p <0.01).

Considerations of Human-influenced Variables

State population, year of state settlement, and state longitude were found to be significantly correlated with introduced species in CONUS, corresponding with Stohlgren et al.'s (2005) observations of a positive correlation between introduced species density and human population density. Correlations were relatively weaker in the EUS but still highly significant, while the WUS results were not significant, likely due to more uniform settlement years and population density values observed among Western states compared to Eastern states. However, since each of these variables is influenced directly or indirectly by humans, they may also be highly correlated with each other. Future analysis will attempt to detect multicollinearity between variables in order to determine what factors are more closely associated with introduced species. The two groupings of "native" and "introduced" species used in this study also limit the level of analysis that can be done due to their generality. Species within each of these groupings may be very dissimilar in their adaptations towards particular climatic or other environmental conditions. Therefore, these results only describe general trends in native or non-native distributions and cannot necessarily be applied to the distribution patterns of specific species.

Human-influenced variables are also approximate indicators of disturbances and plant species introduction. Since the date of introduction for each introduced species is difficult to establish, the year of European settlement in each state was used as an estimate of the earliest possible time of introduction. As the variables tested in this study are not the only factors able influence their distributions, other measures of human influence that may be considered in future analyses include types of land use, such as the presence of agriculture or level of urbanization.

CONCLUSIONS

In this study the latitudinal diversity gradient is supported for native species, but is not observed in introduced species. The lack of a latitudinal diversity gradient observed in native plant species by Stohlgren et al. (2005) likely reflect incomplete county-level data used in their analysis. The use of smaller scale species occurrence data appears to have reduced error from counties underestimating species richness, at the expense of larger scale detail. General patterns of native and introduced species richness are still apparent, however, revealing "hot spots" of introduced species. Since analyses were done at the state level with the use of state centroids for latitude and longitude coordinates, the distribution patterns seen in this study are cannot be directly compared to patterns found in larger scale analyses, but the differences observed between native and introduced species is noteworthy.

The East and West Coasts have the highest concentrations of both native and introduced species, although natives are more likely to be found towards southern states due to the latitudinal gradient. Given the significant correlations between human influences and introduced species, it is possible that this pattern reflects introduction events. This is also supported by the lower introduced species richness values seen in interior states, where their distances from major water bodies and major trade or transportation routes would limit opportunities for species introductions. Since multiple factors in this study correspond with the distribution pattern of introduced species, it is expected that other factors not examined contribute to such distributions as well. Future studies will benefit from examining the relationships of other possible climatic and human influences, such as evapotransporation rates, human migration patterns, or international trade and travel. The movement of introduced species is an ongoing process, with non-native species regularly entering the US and continuing to proliferate and increase their ranges. Given the spatial nature of species invasion, geographic factors will continue to exert a significant influence on species distributions across the United States.

REFERENCES

Blumler, M. 2006. Geographic aspects of invasion: The annual bromes. *Middle States Geographer* 39:1-7.

Denslow, M. W., M. W. Palmer, Z. E. Murrell. 2010. Patterns of native and exotic vascular plant richness along an elevational gradient from sea level to the summit of the Appalachian Mountains, U.S.A. *Journal of the Torrey Botanical Society* 137(1): 67-80.

Flather, C. H., T. J. Stohlgren, C. Jarnevich, D. Barnett, and J. Kartesz. 2006 Plant species invasions along the latitudinal gradient in the United States: Reply. *Ecology* 87(12): 3213-3217.

Fridley, J. D. 2008. Of Asian forests and European fields: Eastern U.S. plant invasions in a global floristic context. *PLoS One* 3 (11): e3630.

Fridley, J. D., H. Qian, P. S. White, and M. W. Palmer. 2006. Plant species invasions along the latitudinal gradient in the United States: Comment. *Ecology* 87(12): 3209-3213.

Glenn-Lewin, D. C. 1977. Species diversity in North American temperate forests. *Vegetatio* 33: 153-162.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *The American Naturalist* 163(2): 192-211.

Jarnevich, C. S., T. J. Stohlgren, D. Barnett, and J. Kartesz. 2006. Filling in the gaps: Modelling native species richness and invasions using spatially incomplete data. *Diversity and Distributions* 12: 511–520.

Lundgren, M. R., C. J. Small, and G. D. Dreyer. 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. *Northeastern Naturalist* 11 (3): 313-332.

Mabry, C. Background and Methods of Control for Garlic Mustard. The Sierra Club. 7 April 2003. <http://www.ci.des-moines.ia.us/departments/pr/projectsandeducation/pdf/garlicmustardreport.pdf>

MacArthur, R. H. and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton: Princeton UP.

Mortensen, D. A., E. S. J. Rauschert, A. N. Nord, and B. P. Jones. 2009. Forest roads facilitate the spread of invasive plants. *Invasive Plant Science and Management* 2: 191-199.

Palmer, M. W. 1995. How should one count species? *Natural Areas Journal* 15: 124-135.

Qian, H. 1999. Spatial pattern of vascular plant diversity in North America north of Mexico and its floristic relationship with Eurasia. *Annals of Botany* 83: 271-283.

Qian, H., J. D. Fridley, and M. W. Palmer. 2007. The latitudinal gradient of species-area relationships for vascular plants of North America. *The American Naturalist* 170: 690-701.

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. New York: Cambridge UP.

Stevens, G. R. 1989. The latitudinal gradient in geographic range: How so many species coexist in the tropics. *The American Naturalist* 133(2): 240-256.

Stohlgren, T. J., D. Barnett, C. Flather, J. Kartesz, B. Peterjohn. 2005. Plant species invasions along the latitudinal gradient in the United States. *Ecology* 86(9): 2298-2309.

Thuiller, W., D. M.Richardson, P.Pysek, G. F.Midgley, G. O. Hughes, M. Rouget. 2005. Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* 11: 2234-2250.

Tobler, W. 1970. A computer movie simulating urban growth in the Detroit region. *Economic Geography* 46(2): 234-240.

US Census Bureau. 2011. 2010 Census state area measurements and internal point coordinates. Washington, DC. < http://www.census.gov/geo/www/2010census/statearea_intpt.html> (last accessed February 2011).

USDA, NRCS. 2010. The PLANTS Database. National Plant Data Center, Baton Rouge, LA. <http://plants.usda.gov> (last accessed November 2010).