

## *PLANT SPECIES INVASIONS ALONG THE LATITUDINAL GRADIENT IN THE UNITED STATES: COMMENT*

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Few biogeographic patterns have been as well documented as the latitudinal gradient in species richness. For North American plants, the decrease in number of species from the subtropics to the arctic is well established (Stevens 1989, Currie 1991, Qian 1999), but becomes less defined as the spatial grain of species richness decreases (e.g., Monk 1967, Glenn-Lewin 1977). There is considerable interest among biogeographers and community ecologists as to whether clear latitudinal patterns are manifest at relatively fine spatial resolutions, where the signature of local processes such as historical disturbances or fine-scale environmental variation could obscure broad-scale geographic drivers of richness (Rahbek and Graves 2001, Whittaker et al. 2001). Because adequate data have generally been lacking, however, there remained until recently no systematic attempt to address the latitudinal gradient of plant richness for the full extent of the United States using relatively fine-scale data.

Stohlgren et al. (2005) examined native and exotic vascular plant species richness at the county level for the 48 conterminous U.S. states in relation to latitude, climate, topographic and biotic factors, and human disturbance. By comparing a variety of multifactor models explaining native and exotic plant richness, Stohlgren et al. (2005) concluded that: (1) there is no relationship between native plant richness and latitude at the county level; (2) the strongest single predictor of exotic species richness is native species richness; and (3) bird species richness, a surrogate for habitat heterogeneity, is the best predictor of native plant richness. If

true, these observations would represent a major advance in the study of plant diversity patterns, as they would suggest scale thresholds where broad-scale geographic patterns are no longer manifest due to the increasing importance of other factors such as local habitat heterogeneity. However, we argue that these conclusions are inaccurate, stemming from uncritical evaluation of completeness in the data set and from artifacts deriving from inappropriate data transformation. Furthermore, we analyze a more appropriate data set to the issue of county-level patterns of native and exotic species richness, and obtain different results than that of Stohlgren et al. (2005).

A major conclusion of Stohlgren et al. (2005:2301) is that “regression analyses showed no relationship between latitude and native plant species density (richness).” We assert that this result is an artifact of two major deficiencies in their study; namely, that (1) their data set of county richness values underestimates true county richness, and (2) richness values were incorrectly transformed to account for variation in survey area. Plant data used by Stohlgren et al. (2005) come from the Biota of North America Program (BONAP), a collection of taxon occurrences from the literature and from herbarium surveys recorded by county (Stohlgren et al. 2003). These data are widely regarded as the “standard plant data set for many government and non-government agencies” (Stohlgren et al. 2005:2299), and we agree that this is the most comprehensive collection of plant occurrence records for North America. However, records for many counties were not themselves collected with the aim of providing complete floristic lists of counties (see Palmer 1995). Thus, although some counties are well collected, others remain less well described for a variety of reasons (such as low survey effort). In addition to adding error to the assessment of county-level richness patterns (thereby undermining the signal of geographic pattern in the data), variation in floristic completeness among counties could cause spurious correlations between native and exotic richness; as well-surveyed counties are more likely to contain more occurrences of both native and exotic species. The use of such data for the analysis of richness patterns is appropriate if researchers make sufficient attempts to correct for, or are at least be able to quantify, the variation in floristic completeness among counties. Stohlgren et al. (2005) give no assessment of data quality in their analysis. Moreover, the only attempt made to reduce the bias associated with including poorly surveyed counties is the removal of 114 counties with fewer than 100 occurrences. This procedure is both insufficient (114 is <4% of the data set) and flawed, in that occurrences are a function of both survey effort and

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actual floristic richness; omission of counties based on low occurrences will spuriously remove legitimate but less rich county richness estimates.

The conclusions of the paper are further eroded by the decision of Stohlgren et al. (2005) to model plant species “density,” rather than raw richness values, by simply dividing county richness by county area (see Gotelli and Colwell 2001). Species richness and area are not linearly related but are most commonly described by the power function  $S = cA^z$  (Arrhenius 1921, Rosenzweig 1995). The transformation applied by Stohlgren et al. (2005) essentially assumes that the richness accumulation rate with area ( $z$ ) is 1, which is a minimum of 4–5 times higher than that commonly reported for county- and state-sized areas (typically between 0.1 and 0.2; Rosenzweig 1995). As a result, larger counties are heavily penalized in their species richness estimates (particularly those in western states and eastern states like Florida and Maine) while those in states of small counties (e.g., Georgia, Indiana, Ohio) get spuriously high values. As there are clear geographic gradients in county size in the United States, this transformation severely inhibits Stohlgren et al. (2005) from uncovering true geographic patterns of county-level richness. It comes as no surprise, then, that this flawed and geographically biased transformation leads Stohlgren et al. (2005) to conclude that there is no latitudinal pattern in richness at the U.S. county level.

The flawed area transformation of richness values also leads to a spuriously strong correlation between native and exotic richness, and between native plant and bird richness. Because all three variables (native plant richness, exotic plant richness, bird richness) are transformed in the same way, they have a built-in correlation that, as we demonstrate, inflates the strength of each relationship. Moreover, with identical transformation, the correlation of these variables is maintained, while their fit to other potentially strong variables (such as climate factors) is diminished, giving the appearance that climate variables are worse predictors of diversity than these “biotic” variables. In addition, counties that are well surveyed for native species are likely to be well surveyed for exotic species, contributing to an artificially high correlation between these variables. Our revised analysis suggests that native and exotic species richness at the county level are far less correlated than suggested by the analysis of Stohlgren et al. (2005). Indeed, even Stohlgren et al. (2005) assert that native and exotic plant richness patterns are explained by very different models; considering this plus artifacts introduced by data transformation, we assert that native and exotic plant richness at the county level are unlikely to be as tightly coupled ( $R^2 = 0.9$ ) as they report.

To provide a more accurate assessment of plant richness patterns at the county level, we have taken a subset of data from the Floras of North America Project

(Withers et al. 1998, Palmer 2005) to address the county-level latitudinal pattern with more adequate data. The database of the Floras project includes >2700 areas that were surveyed specifically for documenting the vascular flora of a defined location. Although no flora is a perfect representation of the total taxonomic richness of a particular area, taxonomic completeness is usually a goal of a floristic survey (Palmer et al. 1995). Each record summary from the Floras project includes total vascular plant species, exotic species, area, geographic location, and date of publication. From this database we selected floras that are roughly county sized, between 50 km<sup>2</sup> and 25 000 km<sup>2</sup> with a mean of 2965 km<sup>2</sup> (conterminous U.S. county range is from 59 to 52 000 km<sup>2</sup> with a mean of 2500 km<sup>2</sup>). We excluded floras that were small islands or peninsulas or did not represent contiguous areas, those that were entirely within wetlands, and those that were published before 1950. Our final set includes 600 floras covering the full extent of North America north of Mexico, including 541 from the conterminous United States (Fig. 1). Note that spatial gaps in Fig. 1 do not necessarily indicate historical gaps of botanical exploration; the floras could have been written before 1950, or for larger (e.g., state) or smaller areas. In addition, although more recent floras should generally be more complete floras, there is no temporal trend in exotic richness in our post-1950 data set ( $P > 0.12$  in a linear model of log(exotic richness) over time; see also Palmer [2005]).

To evaluate the latitudinal gradient in native plant species richness we first standardized richness estimates to a common area using an empirically derived species–area relationship. We used the common log transformation of the power law,  $\log S = \log c + z(\log A)$ , to estimate parameter  $z$  via linear regression of the 600 observed area and richness values. Our calculated  $z$  (=0.158) was then used to transform all richness estimates to that of the geometric mean area in our data set (equivalent to 1074 km<sup>2</sup>), using the formula  $\log S_c = z(\log A_{\text{mean}} - \log A) + \log S$ . We then modeled corrected native richness (log  $S_c$ ) in response to latitude and longitude, for both the full 600 flora data set and the conterminous U.S. subset of 541 floras corresponding to the spatial extent of the Stohlgren et al. (2005) study (Fig. 2).

For both the full data set and the conterminous U.S. subset, best-fit regression models evaluated by the Akaike Information Criterion include third-order terms for both latitude and longitude (Table 1), and explain 31% and 14% of county-level variance in native richness for North America and the conterminous United States, respectively. Latitude and longitude are significant predictors of native richness, although the nature of their effects depends on which data set is used (Table 1). The latitudinal gradient is much stronger when Canada and Alaska are included (Fig. 2); when confined to the

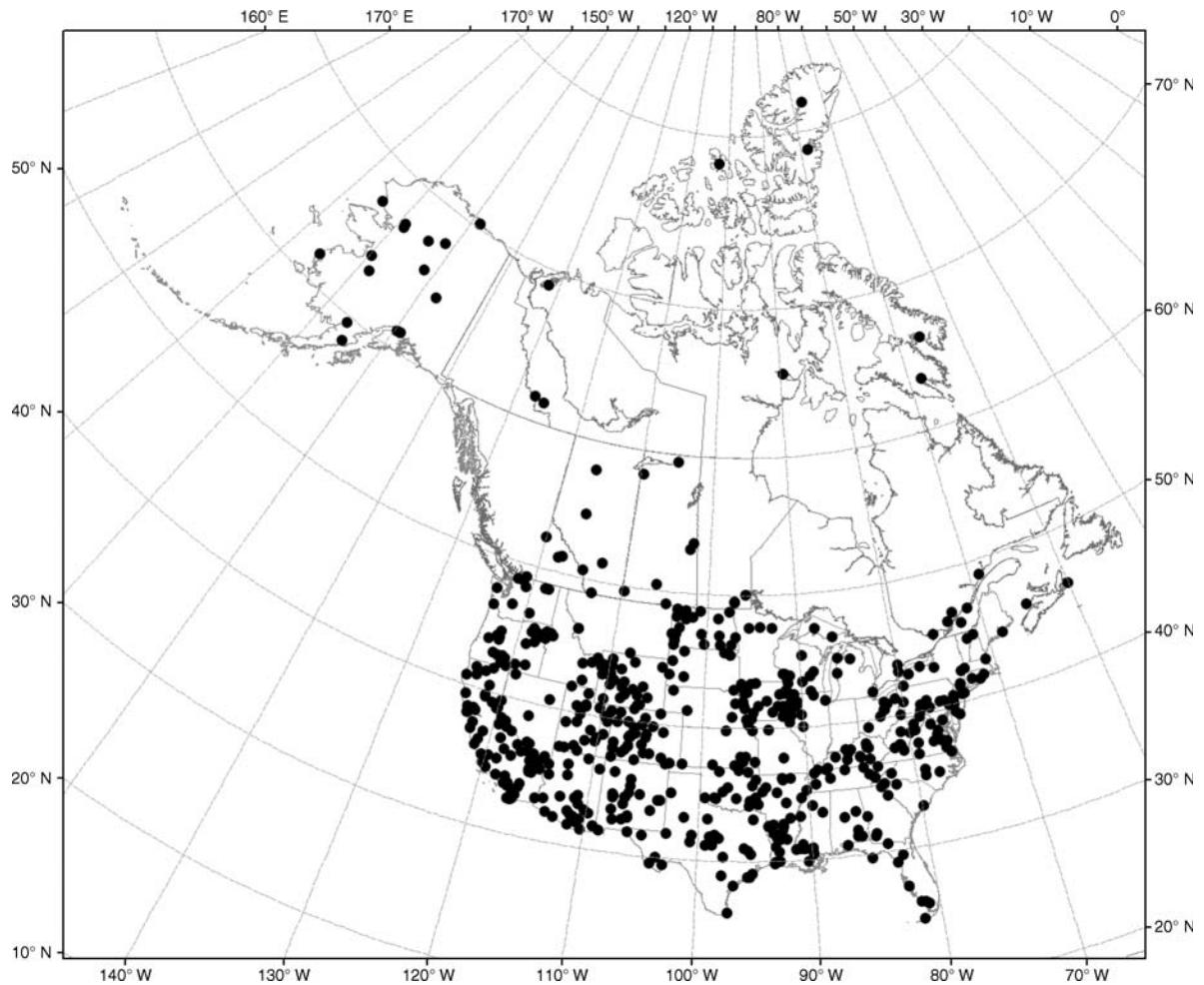


FIG. 1. Locations of 600 county-sized floras from the Floras of North America Project (Withers et al. 1998, Palmer 2005).

latitudes of the conterminous United States, richness decreases weakly and monotonically with latitude, while significant higher order effects emerge with a larger latitudinal range. Significant third-order effects of longitude are detectable in both data sets, where richness is significantly higher along eastern and western coasts. Similar models, but for exotic species richness, contain significant effects of longitude but not latitude.

Although native and exotic species richness are correlated in our data set, the tightness of this relationship is much less than that reported by Stohlgren et al. (2005). When we standardize exotic richness to a constant area (using a fitted  $z$  value of 0.212 relating exotic richness and flora area), native richness explains 44% of the variance in area-standardized exotic richness at the county level (Fig. 3), as opposed to the 90% reported by Stohlgren et al. (2005). If instead we use the approach of Stohlgren et al. (2005) of dividing raw native and exotic richness values by flora area, the

variance in exotic richness explained by native richness is artificially enhanced to 74%. Combined with the likely variation in completeness of county lists in the BONAP data, the flawed area transformation of both native and exotic richness by Stohlgren et al. (2005) produces native–exotic richness correlations that are much higher than we believe actually exist in county-level distribution patterns. Although native and exotic plant richness are likely to respond similarly to many environmental factors, we find it likely that other human and historical factors will ultimately prove to be the most powerful predictors of exotic species distributions (Rejmánek 2004, Taylor and Irwin 2004).

We conclude that, contrary to the conclusions of Stohlgren et al. (2005), there is a significant relationship between latitude and native plant richness at the county level for the conterminous United States. The latitudinal gradient is stronger when latitudes above the conterminous United States are considered, which represents a

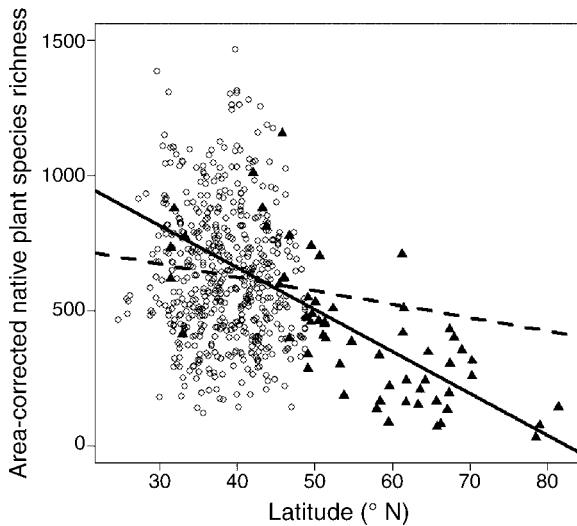


FIG. 2. Relationship between native plant species richness and latitude in 600 county-sized floras for North America (all points, circles and triangles), and for only those floras (541) within the conterminous United States (open circles, dashed regression line). Richness has been corrected to a standard area. Lines represent linear least-squares regressions.

spatial extent not addressed by Stohlgren et al. (2005). Nonetheless, reestablishment of a well-known global pattern at a relatively fine spatial resolution for plants of the United States suggests that broad-scale richness drivers such as climate still play a considerable role in

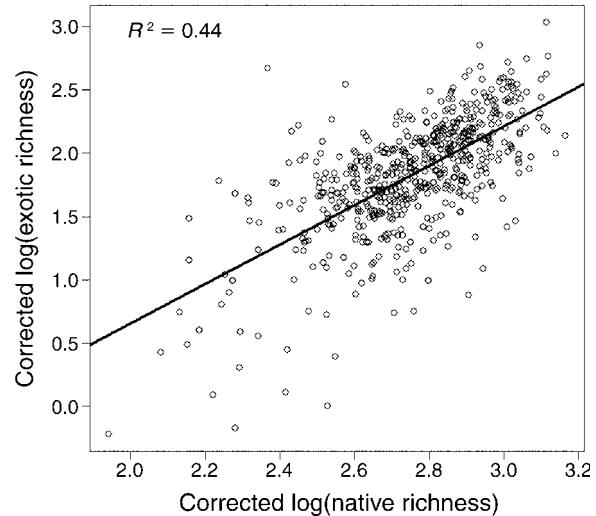


FIG. 3. Relationship between exotic and native plant species richness in 600 county-sized floras from North America, assessed by independently standardizing native and exotic richness to a constant area using an empirically derived species–area relationship. The line represents linear least-squares regression.

the structure of county-sized plant assemblages. This does not preclude a significant role for landscape heterogeneity and environmental favorableness in the fine-scale distribution of species richness: to the contrary, we foresee significant advancement in the under-

TABLE 1. ANOVA results of best-fit models of latitude and longitude predicting area-corrected native species richness in all 600 county-sized floras of (A) North America and (B) a subset of 541 floras from the conterminous United States.

Source of variation	df	ss	ms	F	Coefficient
A) All floras ( $N = 600$ )					
Latitude	1	4.71	4.71	146.28***	0.0678
Longitude	1	0.64	0.64	19.75***	0.1264
Latitude <sup>2</sup>	1	1.41	1.41	43.79***	-0.0024
Longitude <sup>2</sup>	1	0.92	0.92	28.49***	$8.893 \times 10^{-4}$
Longitude $\times$ Latitude <sup>2</sup>	1	0.05	0.05	1.68	$4.168 \times 10^{-6}$
Latitude $\times$ Longitude <sup>2</sup>	1	0.03	0.03	0.99	$-3.767 \times 10^{-7}$
Latitude <sup>3</sup>	1	0.16	0.16	5.12*	$1.541 \times 10^{-5}$
Longitude <sup>3</sup>	1	0.33	0.33	10.29**	$2.457 \times 10^{-6}$
Latitude $\times$ Longitude	1	0.05	0.05	1.63	$-7.653 \times 10^{-4}$
Residuals	591	19.04	0.03		
B) Conterminous U.S. floras only ( $N = 541$ )					
Latitude	1	0.14	0.14	4.85*	0.1504
Longitude	1	0.85	0.85	28.63***	-0.4761
Latitude <sup>2</sup>	1	0.04	0.04	1.48	$-2.963 \times 10^{-4}$
Longitude <sup>2</sup>	1	0.86	0.86	28.97***	$-4.543 \times 10^{-3}$
Longitude $\times$ Latitude <sup>2</sup>	1	0.06	0.06	2.00	$2.312 \times 10^{-5}$
Latitude $\times$ Longitude <sup>2</sup>	1	0.03	0.03	0.97	$2.225 \times 10^{-5}$
Latitude <sup>3</sup>	1	0.03	0.03	0.91	$2.100 \times 10^{-5}$
Longitude <sup>3</sup>	1	0.53	0.53	17.76***	$-1.312 \times 10^{-5}$
Latitude $\times$ Longitude	1	0.04	0.04	1.37	$2.728 \times 10^{-3}$
Residuals	531	15.81	0.03		

Note: Richness was log-transformed.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

standing of richness patterns with the increasing availability of geospatial data and a modeling approach that considers the strong scale dependence of richness patterns. Although we commend Stohlgren et al. (2005) for highlighting the dependence of diversity patterns on scale, a key issue in contemporary ecology (Crawley and Harral 2001, Fridley et al. 2005, Palmer, *in press*), we caution that data transformation must be theoretically sound and completeness must be addressed if we are to understand the scale dependence of ecological phenomena.

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