

## Scale dependence of native and alien species richness in North American floras

Vliv měřítka studia na faktory určující bohatost původních a zavlečených druhů v severoamerických flórách

Michael W. Palmer

Dedicated to Marcel Rejmánek

*Department of Botany, Oklahoma State University, Stillwater, Oklahoma 74078, USA, e-mail: mike.palmer@okstate.edu*

Palmer M. W. (2006): Scale dependence of native and alien species richness in North American floras. – *Preslia* 78: 427–436.

I analyzed data from 1870 vascular floras from regions within North America to assess whether the determinants of native and alien diversity vary as a function of spatial grain. Moving window multiple regression revealed that richness of both native and alien species exhibit the expected species-area relationship, latitudinal gradient, elevation gradient, and year of publication effect. However, the strength of these factors varied between native and alien species, and as a function of scale. Alien diversity was more predictable than native diversity, and is more strongly related to elevation and latitude. For both groups, the latitudinal gradient is most pronounced at broad grains, and the elevational gradient is most pronounced at fine grains.

**Key words:** exotic species, FloraS of North America Project, floristics, native species, spatial scale, species richness

### Introduction

The study of the species-area relationship has yielded a wealth of empirical generalizations and theoretical developments (MacArthur & Wilson 1963, Williams 1964, Rosenzweig 1995, Plotkin et al. 2000, Hubbell 2001, Šizling & Storch 2004). This tradition, as well as the convenience of summarizing the relationship by a simple formula and index ( $z$ ), has largely eclipsed other approaches to understanding the link between biodiversity and scale. Investigations on the components of scale (Palmer & White 1994), landscape geometry (Pyšek et al. 2002, Palmer 2007) and temporal scale (Adler et al. 2005, Fridley et al. 2005) demonstrate that the species-area relationship is not monolithic, and possess a richness that cannot be summarized by a few parameters.

This does not mean that the study of diversity and scale is intractable. Patterns of species richness are often highly predictable (Palmer 1994) based on easily measured geographic factors such as elevation (Rahbek 1995, White & Miller 1988, Vetaas & Grytnes 2002) and latitude (Hillebrand 2004, Hawkins & Agrawal 2005, Stohlgren et al. 2005). Thus, it may be advantageous to examine how richness responds to the scale-dependence of geography.

Palmer (2007) proposed the “environmental texture hypothesis”, which states that the geometry of important environmental variables varies as a function of scale. At both fine and broad scales, the environment varies as a smooth (low fractal dimension) function of space, because of the effects of topography at fine scales and climate at broad scales. This

causes the number of species to be strongly related to area. At intermediate scales, however, the dominant variables (e.g. land use, soil types, topography, disturbance) are more geometrically complex (high fractal dimension). In such a landscape, most of the environmental is “captured” at relatively fine scales – thus adding more area does not add much to the species-area relationship. The environmental texture hypothesis predicts that species-area relationships will be intimately linked with the fractal dimension of each region.

While traditional ecological thought predicts a negative relationship between alien and native diversity (e.g. Elton 1958) there is strong empirical support for a positive relationship (Stohlgren et al. 1999). This implies a common set of factors determine both alien and native diversity. However, the strength of the relationship varies as a function of spatial grain (Stohlgren et al. 2003) implying there may be scale-dependent differences between native and alien species in the determinants of biological diversity.

The purpose of this study is to use data from 1870 published floras from North America, and to examine whether the relationship between species richness and latitude, elevation, and publication year varies as a function of spatial grain.

## Methods

### *The data set*

The data used are derived from the FloraS of North America project. The ‘S’ is capitalized to distinguish it from the Flora of North America project (Flora of North America Editorial Committee 1993). These floras were obtained by standard library searches (electronic and otherwise), bibliographies, and other means. Among other variables, we extracted the following from each flora where possible: number of native species, number of alien species, area, minimum and maximum latitude and longitude (or where not available, geographic midpoints), minimum and maximum elevation, and year of publication. While the project is only about 50% complete, there are usable data from 1870 floras. These floras include plant lists from bogs, outcrops, valleys, mountains, parks, refuges, preserves, counties, states, provinces, countries, and a broad diversity of other defined regions. Data from ecological plots are not included in this study. Floras range over 12 orders of magnitude in spatial scale, and span the continent of North America, north of Mexico. Further details are available in Withers et al. 1998, Palmer 2005, Palmer 2007, and <http://botany.okstate.edu/floras/>.

I calculated geographic midpoints from the minima and maxima, as well as the midpoint of the elevational range. I log-transformed area, and  $\log(x + 1)$  transformed native and alien species richness. The “+1” is necessary because alien species richness is occasionally zero.

All logarithms are common (i.e. base 10). For simplicity, I refer to the mean of the logarithms of the areas in hectares as the “spatial scale”; for example, instead of saying “a mean logarithm of area corresponding to a million hectares” I say “a spatial scale of 6”.

### *Moving-window regressions*

In order to assess scale-dependent changes in determinants of diversity, I ranked the floras by area from smallest to largest. I then performed a series of multiple regressions (separately for native and alien species) with the following model:

$$\text{Log}(\text{richness} + 1) = \beta_0 + \beta_1 \log(\text{area}) + \beta_2 \text{latitude} + \beta_3 \text{elevation} + \beta_4 \text{year} + \varepsilon$$

The first regression included the 1st through the 400th floras, the second included the 2nd through 401st floras, and so on to the 1471st through the 1870th floras. Thus, I present a total of 2942 multiple regressions, each with  $n = 400$ . I chose  $n = 400$  as a reasonable tradeoff between precision of estimates (which increases with  $n$ ) and the breadth of scales represented among regressions (which decreases with  $n$ ).

To facilitate comparison, I display the  $t$ -values associated with the regression coefficients ( $\beta$ s). Several factors (e.g. lack of independence, nonrandom sampling, nested floras) preclude strict interpretation of statistical significance, so inferential statistics are only presented as an exploratory guide.

I also considered complex models, including range of elevations, longitude, and interactions among terms. While such models yielded insights into the interrelationships among the variables, I do not present them here because of my lack of ingenuity in displaying their outcome. Fortunately, they confirm the broader results of the simple model described here.

The analyses presented here are an attempt at tackling a large, complex, and incomplete data set with many biases. More sophisticated analyses, addressing some of these biases, will be performed once the data set is more complete.

## Results and discussion

### *Range of areas*

Despite the large number (400) of floras being binned for each regression, the range of spatial grains within a bin is small compared to the range among bins (Fig. 1). The bin means range from 0.62 to 6.37, corresponding with areas of slightly more than 4 ha to approximately 2 million ha). The range is narrow at around 5.2 (corresponding approximately to 160,000 ha), which is the size of typical U.S. counties (floras are often written for counties). The greatest ranges are at the smallest and largest spatial scales.

### *Area*

Figures 2–5 represent the  $t$ -values associated with regression coefficients. Since all of the regressions have the same number of observations, they can be compared across grains, regressions and variables.

As expected, area has a positive (or slightly negative) effect on both native and alien richness (Fig. 2). The effect is stronger for native than for alien species; this may be due to many alien species being cosmopolitan weeds. For both groups, there is a “dip” between 5 and 6. This is not surprising, because there is not much variation in scale for those regressions (Fig. 1). There is a strong second dip at a finer grain ( $\sim 3.4$ ) for native richness that is not clearly associated with a lack of variation in scale. This weakness of an area effect at this scale is consistent with the environmental texture hypothesis (Palmer 2007) as discussed in the introduction: the complex geometry of the environment precludes a strong area effect.

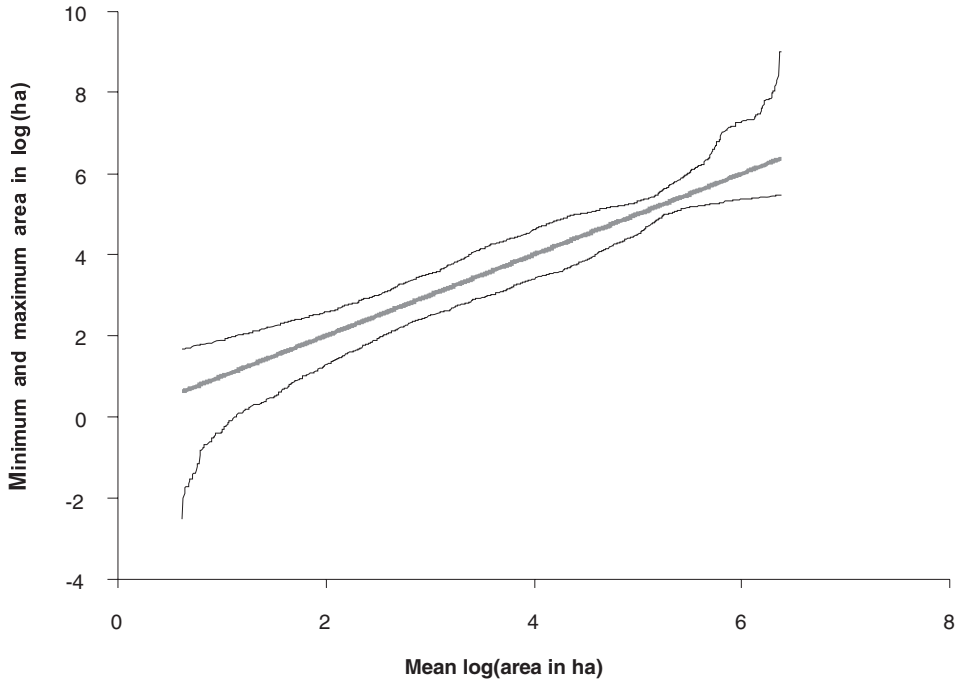


Fig. 1. – Minima (lowest line) and maxima (uppermost line) for groups of 400 floras, arranged from smallest grains to largest. The line in the middle is the line of equality.

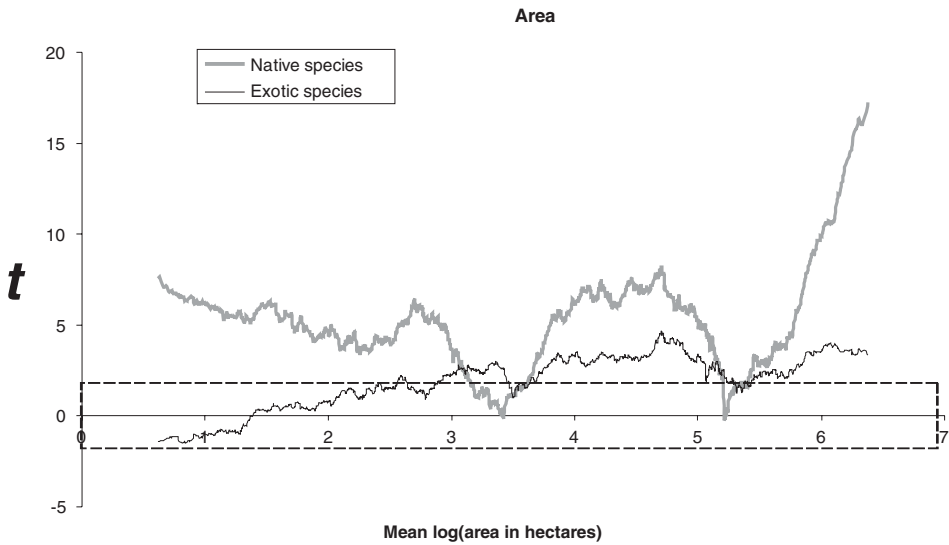


Fig. 2. – *t*-values for the regression coefficient for log(area) in the moving window multiple regressions. The dashed line encloses the 95% confidence interval.

### *Latitude*

Both native and alien species exhibit a strong latitudinal gradient, as evidenced by negative values for  $t$  in Fig. 3. The latitudinal gradient only becomes prominent at scales above 4, and becomes extremely strong at grains above 5.5. The scale-dependence of the latitudinal gradient is equivalent to the latitudinal dependence of the species-area relationship: high latitudes tend to have lower  $z$  coefficients than low latitudes (Drakare et al. 2006).

Compared with the other variables, alien and native species behave very similarly with respect to the latitudinal gradient. However, over most grains, the gradient is stronger for alien species. This is consistent with the observation of many floras at high latitudes with no alien species (Withers et al. 1998). It is not clear how much of this pattern is caused by climatic constraints, and how much is caused by a low magnitude of human activity at high latitudes. Niche-based modeling might resolve such questions (Thuiller et al. 2005).

### *Elevation*

Both native and alien species exhibit the expected elevation gradient (i.e. fewer species at higher elevations; Fig. 4). The gradient is much stronger for alien than for native species. Interestingly, the elevation effect becomes positive for native species at broad grains. This is not surprising, because high elevations are associated with high variation in elevation at broad scales. Higher environmental heterogeneity supports more species (Palmer 1991, Pausas et al. 2003). This effect is apparently not strong enough to reverse the elevation gradient for alien species.

As with latitude, it is unclear whether the strength of the elevation gradient for aliens is mostly due to climatic constraints, or a lower human impact at higher elevations (McKinney 2002).

In contrast to this study, Arévalo et al. (2005) found that alien and native species had similar responses to the elevation gradient in the Canary Islands; however, that study only focused on small grains (i.e. ecological plots).

### *Publication year*

Publication year is generally positively related to species richness (Fig. 5), a probable artifact of the cumulative effect of botanical exploration (Palmer 2005). The slight negative trend for alien species at a fine grain is probably caused by a tendency for recent floristic authors to seek out relatively undisturbed areas for study. Overall, the explanatory value of publication year is weak.

### *Strength of explanatory factors*

Except at the largest grains, variation explained by the four variables is relatively low, as evidenced by the coefficients of determination or  $r^2$  (Fig. 6). Alien species are more predictable than native species, except at the broadest grains. The low variation explained at grains between 5 and 6 is likely due to the low variation in area (Fig. 1). Future research will explore methods to correct for this potential bias.

The low variation explained at a grain of  $\sim 2$  is not surprising, given the multitude of unmeasured factors that can vary at the scale of 100 ha. According to the environmental texture hypothesis (Palmer 2007), we do not expect diversity to be predictably related to geo-

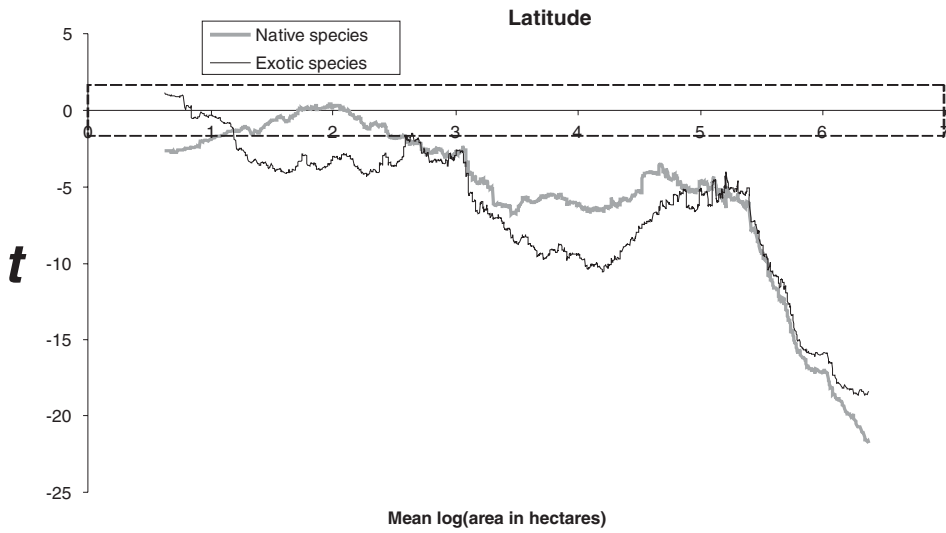


Fig. 3. –  $t$ -values for the regression coefficient for latitude in the moving window multiple regressions. The dashed line encloses the 95% confidence interval.

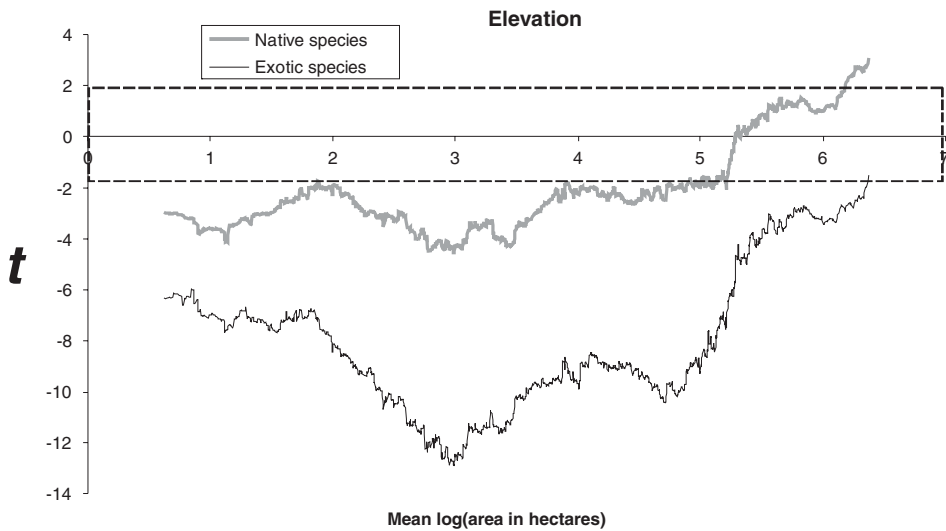


Fig. 4. –  $t$ -values for the regression coefficient for elevation in the moving window multiple regressions. The dashed line encloses the 95% confidence interval.

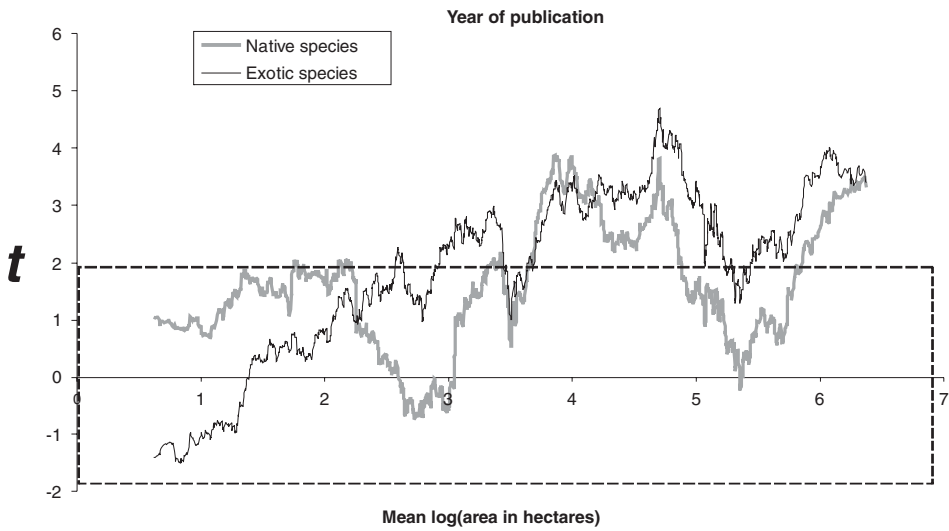


Fig. 5. –  $-t$ -values for the regression coefficient for year of publication in the moving window multiple regressions. The dashed line encloses the 95% confidence interval

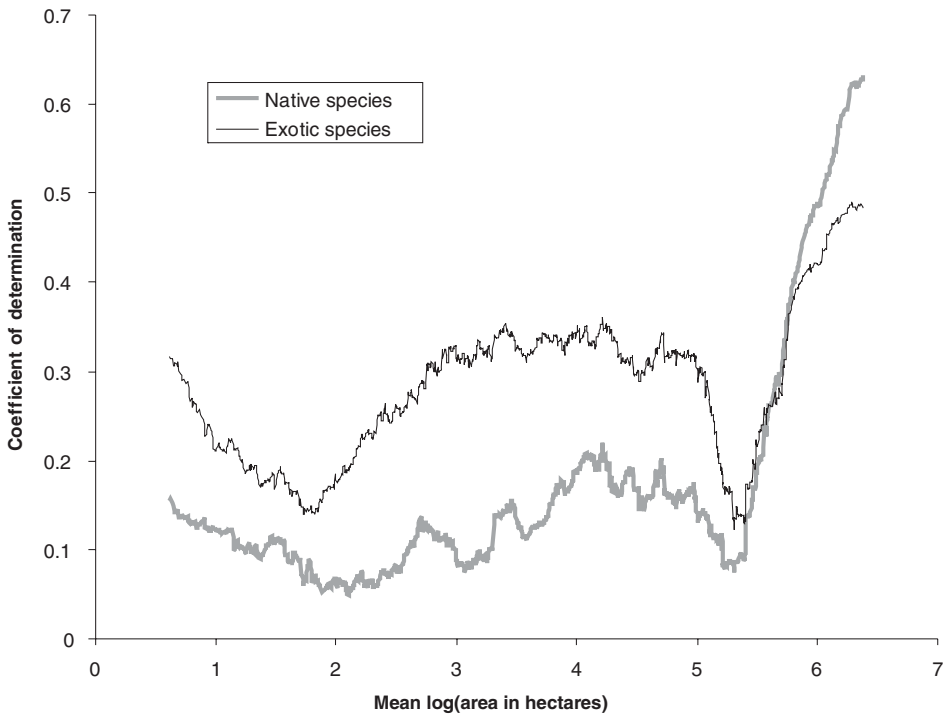


Fig. 6. – Coefficient of determination ( $r^2$ ) for the moving window multiple regressions, including area, latitude, elevation, and year of study as explanatory variables.

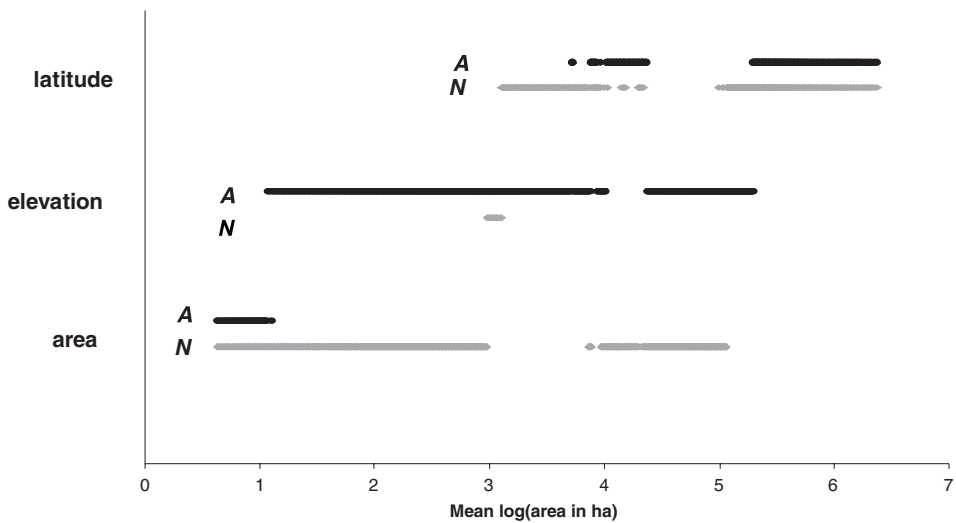


Fig. 7. – The variables most important in explaining species richness, as indicated by the maximum value of the absolute value of  $t$ , as a function of spatial grain. Publication year was never the most important variable, so it is not indicated here. A = alien species richness; N = native species richness.

graphic trends at such scales. At such scales, variables such as land use and soil chemistry may have more explanatory power – but since the “important” variables will vary among sites, a global analysis is infeasible at present.

For both native and alien species, area is the strongest factor related to species richness at the finest grains, and latitude is the strongest at the broadest grains (Fig. 7). Nevertheless, the differences between the groups are striking. Area is only important for alien species at the finest scales, while elevation is important at most scales. Elevation is almost never the dominant factor for native species.

## Conclusions

With a few exceptions, the richness of alien and native species respond in similar directions to similar factors. As expected, richness of both groups is generally positively correlated with elevation and year of study, and negatively correlated with latitude and elevation. These common responses are sufficient to create a strong positive correlation between native and alien species richnesses (it should be noted, that the high correlations remain even after the explanatory variables are factored out).

Despite the superficial similarity in response, there are profound differences between native and alien species in the explanatory value of different factors. For example, alien species experience stronger latitudinal and elevation gradients than native species. Furthermore, the importance of such factors varies strikingly as a function of grain.



The science of biodiversity cannot be readily decoupled from the science of spatial scale (Palmer & White 1994, Chalcraft et al. 2004, Rahbek 2005). There is greater depth to the scale/depth relationship than the  $z$  coefficients of species-area curves. We are stymied by a lack of methodology for addressing such scaling issues. Moving window regression, as illustrated here, represents one technique for our scaling toolbox. New methodologies are needed to help correct acknowledged biases and other data problems without introducing new ones (Gotelli & Colwell 2001, Williamson et al. 2001).

## Acknowledgements

I wholeheartedly thank people who have provided me with floras, bibliographies of floras, or other assistance. These include Daniel McGlenn, Kyanna Cherry, Nick Rasmussen, Karen Ray, Sophonia Roe, Kristin Kegler, Steve McLaughlin, Akbar Syed, Alan Weakley, Bill Lehman, Steven Hill, Will Lowry, Carolyn Klink, Tatsuro Yamada, Bruce Connery, Catherine Hovanic, Garrett Crow, Jim Hull, Louis Iverson, Kathryn Mauz, Kelly Allred, Martin Zocher, P. K. Work, Richard Mitchell, Sandra Peterson, Steven Hull, Hong Qian, Jason Fridley, Ronald Hartman, Neil Snow, Peter White, Paul Neal, Mark Withers, Gary Wade, Donna Ford-Werntz, Glen Rink, John Hayden, David Maxwell, Sandrine Casanova, Stephanie Glenn, Bruce Hoagland, and many others. Comments from an anonymous reviewer and editor Petr Pyšek are gratefully acknowledged. Financial support in the past has come from the OSU College of Arts and Sciences, the U.S. Forest Service, the National Biodiversity Information Infrastructure as administered through the Houston Advanced Research Center.

## Souhrn

Práce na základě analýzy 1870 flór cévnatých rostlin z území Severní Ameriky ukazuje, jak se faktory určující bohatost původních a zavlečených druhů mění s prostorovým měřítkem studia. Mnohorozměrná regrese ukázala, že mezi bohatostí obou skupin druhů existuje očekávaný vztah, ovlivněný gradientem zeměpisné šířky, nadmořské výšky a rokem publikace. Vliv těchto faktorů na původní a zavlečené druhy byl však různě silný a závisel na měřítku studia. Diverzita nepůvodních druhů byla pomocí zahrnutých faktorů lépe předpověditelná a vykazovala těsnější vztah k nadmořské výšce a zeměpisné šířce. V obou skupinách měl gradient zeměpisné šířky výraznější vliv na druhovou diverzitu při větším měřítku, zatímco nadmořská výška na jemnější prostorové škále.

## References

- Adler P. B., White E. P., Lauenroth W. K., Kaufman D. M., Rassweiler A. & Rusak J. A. (2005): Evidence for a general species-time-area relationship. – *Ecology* 86: 2032–2039.
- Arévalo J. R., Delgado J. D., Otto R., Naranjo A., Salas M. & Fernández-Palacios J. M. (2005): Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). – *Persp. Plant Ecol. Evolut. Syst.* 7: 185–202.
- Chalcraft D. R., Williams J. W., Smith M. D. & Willig M. R. (2004): Scale dependence in the species-richness-productivity relationship: The role of species turnover. – *Ecology* 85: 2701–2708.
- Drakare S., Lennon J. J. & Hillebrand H. (2006): The imprint of the geographical, evolutionary and ecological context on species-area relationships. – *Ecol. Lett.* 9: 215–227.
- Elton C. (1958): The ecology of invasions by animals and plants. – Methuen & Co., London.
- Flora of North America Executive Committee (1993): Flora of North America. – Oxford University Press, New York.
- Fridley J. D., Peet R. K., Wentworth T. R. & White P. S. (2005): Connecting fine- and broad-scale species-area relationships of Southeastern US Flora. – *Ecology* 86: 1172–1177.
- Gotelli N. J. & Colwell R. K. (2001): Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. – *Ecol. Lett.* 4: 379–391.
- Hawkins B. A. & Agrawal A. A. (2005): Latitudinal gradients. – *Ecology* 86: 2261–2262.
- Hillebrand H. (2004): On the generality of the latitudinal diversity gradient. – *Amer. Natur.* 163: 192–211.
- Hubbell S. P. (2001): The unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press, Princeton.
- MacArthur R. & Wilson E. O. (1963): An equilibrium theory of insular zoogeography. – *Evolution* 17: 373–387.

- McKinney M. L. (2002): Influence of settlement time, human population, park shape and age, visitation and roads on the number of alien plant species in protected areas in the USA. – *Diversity Distrib.* 8: 311–318.
- Palmer M. W. (1991): Patterns of species richness among North Carolina hardwood forests: tests of two hypotheses. – *J. Veget. Sci.* 2: 361–366.
- Palmer M. W. (1994): Variation in species richness: towards a unification of hypotheses. – *Folia Geobot. Phytotax.* 29: 511–530.
- Palmer M. W. (2005): Temporal trends of exotic species richness in North American floras: an overview. – *Ecoscience* 12: 386–390.
- Palmer M. W. (2007): Species-area curves and the geometry of nature. – In: Storch D., Marquest P. A. & Brown J. H. (eds.), *Scaling biodiversity*, Cambridge Univ. Press, Cambridge (in press).
- Palmer M. W. & White P. S. (1994): Scale dependence and the species-area relationship. – *Amer. Natur.* 144: 717–740.
- Pausas J. G., Carreras J., Ferr A. & Font X. (2003): Coarse-scale plant species richness in relation to environmental heterogeneity. – *J. Veget. Sci.* 14: 661–668.
- Plotkin J. B., Potts M. D., Leslie N., Manokaran N., LaFrankie J. & Ashton P. S. (2000): Species area curves, spatial aggregation, and habitat specialization in tropical forests. – *J. Theor. Biol.* 207: 81–99.
- Pyšek P., Kučera T. & Jarošík V. (2002): Plant species richness of nature reserves: the interplay of area, climate and habitat in a central European landscape. – *Global Ecol. Biogeogr.* 11: 279–289.
- Rahbek C. (1995): The elevational gradient of species richness: a uniform pattern? – *Ecography* 18: 200–205.
- Rahbek C. (2005): The role of spatial scale and the perception of large-scale species-richness patterns. – *Ecol. Lett.* 8: 224–239.
- Rosenzweig M. L. (1995): *Species diversity in space and time*. – Cambridge Univ. Press, Cambridge.
- Šizling A. L. & Storch D. (2004): Power-law species-area relationships and self-similar species distributions within finite areas. – *Ecol. Lett.* 7: 60–68.
- Stohlgren T. J., Barnett D., Flather C., Kartesz J. & Peterjohn B. (2005): Plant species invasions along the latitudinal gradient in the United States. – *Ecology* 86: 2298–2309.
- Stohlgren T. J., Barnett D. T. & Kartesz J. (2003): The rich get richer: patterns of plant invasions in the United States. – *Front. Ecol. Environ.* 1: 11–14.
- Stohlgren T. J., Binkley D., Chong G. W., Kalkhan M. A., Schell L.D., Bull K. A., Otsuki Y., Newman G., Bashkin M. & Son Y. (1999): Exotic plant species invade hot spots of native plant diversity. – *Ecol. Monogr.* 69: 25–46.
- Thuiller W., Richardson D. M., Pyšek P., Midgley G. F., Hughes G. O. & Rouget M. (2005): Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. – *Global Change Biol.* 11: 2234–2250.
- Vetaas O. R. & Grytnes J. A. (2002): Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. – *Global Ecol. Biogeogr.* 11: 291–301.
- White P. S. & Miller R. I. (1988): Topographic models of vascular plant richness in the southern Appalachian high peaks. – *J. Ecol.* 76: 192–199.
- Williams C. B. (1964): *Patterns in the balance of nature*. – Academic Press, New York.
- Williamson M., Gaston K. J. & Lonsdale W. M. (2001): The species-area relationship does not have an asymptote! – *J. Biogeogr.* 28: 827–830.
- Withers M. A., Palmer M. W., Wade G. L., White P. S. & Neal P. R. (1998): Changing patterns in the number of species in North American floras. – In: Sisk T. D. (ed.), *Perspectives on the land-use history of North America: A context for understanding our changing environment*, p. 23–32, USGS, Biological Resources Division, Denver.

Received 18 July 2006

Revision received 14 September 2006

Accepted 18 September 2006