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

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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.

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DENSLOW M. W. (Department of Biology, Appalachian State University, Boone, NC 28608), M. W. PALMER (Department of Botany, Oklahoma State University, Stillwater, OK 74078), AND Z. E. MURRELL (Department of Biology, Appalachian State University, Boone, NC 28608). 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. J. Torrey Bot. Soc. 137: 67–80. 2010.—We used floristic studies from the state of North Carolina to compare the patterns of total, native and exotic plant species richness from sea level (Atlantic coast) to the summit of the Appalachian Mountains. Few studies have investigated how patterns of native and exotic species richness differ along environmental gradients, and these studies have yielded contrasting results. We compare our results with those few published studies, and demonstrate that there is a need for future studies examining exotic richness along gradients. We modeled the effects of size of study area, year of study, and elevation on species richness using a dataset of sixty-eight floristic studies. Native and exotic species richness showed a positive relationship with area and year. Exotic species showed a steeper slope than native species for the species-area relationship. Richness of both groups was positively but weakly related to year of study. After accounting for area and year, native species displayed a hump-shaped pattern along the elevational gradient. Exotic species richness was weakly related to elevation, which was not a significant variable in the model. This contrasts with the few previous studies that have examined exotic richness patterns along elevational gradients that have found either a strong linear decline, or a strong hump-shaped pattern. Both native and exotic species showed high variation in richness at elevations below 400 m. We conclude that different processes may govern native and exotic plant richness patterns and that exotic richness patterns along gradients may in fact be idiosyncratic due to factors such as disturbance history.

Key words: Appalachian Mountains, elevation, exotic, gradient, human impact, native, plants, restricted cubic spline, species-area relationship, species richness.

The response of species diversity to physical and environmental gradients has played a central role in ecological research and the development of theory (MacArthur and Wilson 1967, Rosenzweig 1995). In particular, studies of species-area relationships and elevational gradients have received much attention (Rahbek 1995, Palmer 2007). In fact, the species-area relationship (the fact that larger areas harbor more species) is one of ecology's most general patterns (Rosenzweig 1995),

though the details and causes of this relationship remain an area of active research.

Species richness generally decreases from low to high elevations. However, the shape of this relationship varies from humped to monotonic (Nogués-Bravo et al. 2008). Previous studies have suggested that some of the contrasting patterns of richness along elevation may depend on the length of the sampled gradient or other sampling effects (Rahbek 1995, Lomolino 2001, Nogués-Bravo et al. 2008). A review of 204 studies conducted along elevational gradients indicated that a hump-shaped pattern is the most typical pattern, with a monotonic pattern also frequently encountered (Rahbek 2005). However, when complete gradients are sampled a hump-shaped pattern is expected for plants and vertebrate taxa. In order to detect hump-shaped patterns data collection should span the entire gradient or at least the part of the

gradient where peaks are expected to occur (Rahbek 2005).

Explanations for elevational trends in richness tend to fall into four categories: historical, climatic, biotic, and spatial (Grytnes and McCain 2007, McCain 2007). Historical explanations focus on processes that occur in geologic history and over evolutionary time scales (e.g., niche conservatism, Mittelbach et al. 2007; quaternary climate, Araújo et al. 2008). Climatic explanations emphasize current climatic conditions as the primary determinants of species richness. Climate patterns can vary between regions and interactions between climatic variables (e.g., temperature and rainfall) can be particularly important (McCain 2007). Biotic explanations, such as the mass-effect, or the establishment of species in areas where self-maintaining populations cannot exist, have been observed in some areas (e.g., Grytnes et al. 2008b). Spatial hypotheses such as spatial constraint (the mid-domain effect) have generated considerable examination and debate (Hawkins et al. 2005 and references therein). The mid-domain effect predicts a hump-shaped species richness pattern when species ranges are randomly distributed within a geometrically constrained area (i.e., coast to mountain top). There has been conflicting evidence for the mid-domain effect; it has been found to be important in some cases (plants on Mount Kinabalu; Grytnes et al. 2008a) and is not supported in others (ants in the Great Smoky Mountains, Sanders et al. 2007). Though historical, climatic, biotic and spatial explanations have been used individually to explain elevational richness patterns, these processes may actually work collectively or interactively along environmental gradients (Lomolino 2001, Grytnes and McCain 2007, Körner 2007).

Previous studies of richness gradients (e.g., species-area relationship, latitude, elevation) have generally focused on total species richness, and relatively few have investigated how patterns of native and exotic species richness differ (Sax and Gaines 2006). Investigations of exotic species have proved historically important to the understanding of the natural world (Sax et al. 2007). For example, Charles Darwin (Darwin 1859) gained insights into biogeography from his observations of exotic taxa. Exotic species can be good models for biodiversity analyses for several reasons. For example, if exotic species respond similarly to natives along environmental gradients it may indicate that physical environmental factors are a dominant influence on biotic patterns, with both groups of species responding similarly to environmental conditions. In contrast, if exotic and native species exhibit contrasting richness patterns, competitive processes might limit alien species, (e.g., biotic resistance, Elton 1958). The concept of 'biotic acceptance' posits that areas with high native richness also have high exotic richness (Stohlgren et al. 2006). It should be noted that the relationship of natives to exotics can show strong scale dependence (reviewed in Fridley et al. 2007).

In general, studies that have investigated the patterns of native and exotic richness have not yielded consistent insights. Palmer (2006) found that both native and exotic species showed similar area, latitudinal, and elevational relationships. Blackburn et al. (2007) demonstrated that the species-area relationships of native and exotic species for islands around the world were similar, but the species-isolation relationships were not. Exotic species richness did not decline as a function of distance from the mainland, while native species did. Hulme (2008) found that while native and exotic species both increased with area in the United Kingdom, the slope of this relationship differed across spatial grain. This study also showed consistently steeper slopes for exotic species. This is inconsistent with the findings of Crawley (1987) who found steeper slopes for the native species-area relationship. A shallower slope for exotic species could indicate that they are not as dispersal limited as natives (Rosenzweig 1995, Sax and Gaines 2006).

Exotic richness patterns along latitudinal gradients are an active area of research and debate. Latitudinal gradients of species richness are similar for native and exotic species outside of the tropics, with richness decreasing towards higher latitudes (Sax 2001). In contrast, Stohlgren et al. (2005) found no exotic richness pattern with respect to latitude in the United States. This observation could represent a major contribution to the study of exotic richness along gradients at the broad scale. However, Fridley et al. (2006) felt that the study suffered from methodological flaws, bringing its conclusions into question. Specifically, species richness values were standardized by area (richness was divided by area

within U.S. counties) to obtain a density value and the study made use of an incomplete dataset. An arguably more appropriate transformation and dataset used by Fridley et al. (2006) indicated that exotic species did show the expected latitudinal decrease in richness.

Elevational gradients in exotic species richness remain little explored. The few studies that have examined exotic richness along a large elevational gradient have found either a monotonic decline or a hump-shaped pattern. For example, monotonic declines in exotic species were observed along roadsides and railways sampled from 200–2300 m in the Swiss Alps (Becker et al. 2005). Mallen-Cooper and Pickering (2008) sampled vegetation plots from 540–2020 m in the Snowy Mountains, Australia. They found that both exotic and native species richness showed linear declines with altitude. The rates of decline (slopes) were similar, but the fit (r^2) was better for the exotic models. Arévalo et al. (2005) sampled along a complete elevational gradient from 0–1950 m on the Canary Islands, Spain. They found a mid-elevation peak in species richness for both native and exotic species and the results were quantitatively (r^2) and qualitatively (shape of response) similar. In addition, Tassin and Rivière (2003) found a hump-shaped pattern for exotic plants sampled from 0–3000 m on Reunion Island, France.

This study investigates the pattern of exotic species richness along a complete elevational gradient in eastern North America. In addition, we examine whether native and exotic species show similar richness patterns along the elevational gradient. We assess how well the independent variables (area, year of study, and elevation) predict species richness, using floras (published floristic studies) as data points.

Materials and Methods. LOCATION AND DATASET. The dataset used in this study was derived from floras of North Carolina, U.S.A. Only floras located within a geographic rectangle defined as the area from > 34.7° N latitude to the Virginia border were used. This allowed for more even sampling across the elevational gradient so as not to over represent low elevation areas. The floras were obtained in collaboration with the FloraS of North America project. The capitol 'S' is used to distinguish it from the Flora of North America

project (Flora of North America Editorial Committee 1993). More information of the FloraS of North America project can be found in Palmer (2005) and at http://botany.okstate.edu/floras/. Other floras were obtained from standard literature searches (e.g., Web of Science), bibliographies of known floras and journal scanning (e.g., *Castanea*). Only publications that were stated by the author to be complete representations of a flora were used for the analysis. For example, 'spring floras' or floras that excluded specific taxa (e.g., *Poaceae*) were not used due to incomplete richness values. Island floras were also excluded from the analysis, as these areas may be more strongly governed by dispersal than mainland areas (Rosenzweig 1995) and could therefore obscure elevational patterns.

Species richness data from floras allows for the investigation of elevational patterns of richness across broad scales and grain sizes. An analysis by Nogués-Bravo et al. (2008) found that elevational patterns of total plant species richness may be free of grain size. In other words, the same hump-shaped pattern was found when sampling grain sizes from 1 km² to 81 km². Floras also have the benefit of being representative of the richness of a large area. Each flora represents an intensive investigation of a given location over all seasons and often over multiple years. The use of floras also allows for the investigation of richness trends through time (e.g., Palmer 2005). This does not mean that floras are without bias (Palmer 1995). For example, as with general collecting, floras are not uniformly distributed on the landscape indicating site selection bias (Pautasso and McKinney 2007, Denslow 2009). Nevertheless, floras have tremendous value for the understanding of macroecological patterns (e.g., Kier et al. 2005, Palmer 2006, Kreft et al. 2007, Qian 2009).

For each flora, we determined total vascular plant richness at the species level of natives and exotics, middle elevation of the study area (derived from the minimum and maximum elevation values), area (size of study area) and publication year (or year the study was initiated if more than 2 years prior to the publication date). There are two primary reasons for including year as a variable in the species richness models. First, previous studies have shown that an increase in sampling effort can lead to increases in the

number of recorded species (Palmer 2005, Lobo et al. 2007), suggesting a possible sampling effect of increased numbers of published floras over time. Second, exotic species richness may actually increase with time (independent of any sampling effect) due to ongoing introductions. Exotic species are defined as any species not native to North America. This was determined by consulting the USDA Plants Database (USDA-NRCS 2008). Species listed by the author as only cultivated were excluded from the richness counts.

When different sources of data are used to model species richness there is a chance that the richness counts may be affected by the taxonomic concepts used in the original sources. To evaluate this possibility, the effect of different taxonomic concepts was assessed for five floras from this dataset. The taxonomy was reconciled for five floras and the effect on species richness was determined. The two taxonomic concepts compared were Radford et al. (1968) and Weakley (2008). This analysis indicated that studies at the level of species would not be severely affected by using data from sources with different taxonomic concepts (Appendix A). The difference in richness counts ranged from 0.3% to 2.3%, with a mean difference of 1%. In addition, since log transformations were used, the differences in richness are very small, and are much smaller than the residual errors from the regression models.

We used sixty-eight floras (Appendix B) located along a large elevational gradient (0–2037 m). This gradient ranges from sea level on the coast of North Carolina, U.S.A., to the highest elevation in the eastern United States (Mt. Mitchell). The floras ranged from 2.8–620,000 hectares in size. A large geographic extent was used to encompass the large elevational gradient present in North Carolina. The floras used in this analysis ranged from the year 1901–2006.

Analyses Performed. Total, native, and exotic richness values cannot be modeled directly as a function of elevation because of the important effects of area and year on species richness (Rosenzweig 1995, Palmer 2005). For these reasons, we constructed a linear regression model that included area, year and elevation. We $\log_{10}$ transformed area, exotic, native and total species richness. The

log-transformed power model is one of the most commonly used species-area relationship functions (Arrhenius 1921, Rosenzweig 1995). Species-area relationships generally fit a straight line in log-log space and the power function is suitable for predicting species richness values over ten-fold increases in area (Rosenzweig 1995, Dengler 2009). Adding $\log_{10}$ area and year as covariates accounts for the effect of these variables and tests for the effect of elevation on species richness. As stated previously, the shape of the species richness response to elevation can vary and take different shapes (Rahbek 2005). In order to detect nonlinear effects we add a restricted cubic spline (also called natural spline) to the elevation term. Spline functions are smoothly joined piecewise polynomials used for curve fitting (Durrleman and Simon 1989). Spline functions can approximate the shape of the response better than the addition of polynomial terms in ordinary least squares models (Harrell 2001). For example, polynomials can take on undesirable shapes and the fit in one region of the predictor is strongly affected by the data in other regions of the predictor (Harrell 2001). When using restricted cubic spline functions, the investigator must pre-select the number of knots (join points of piecewise function). We followed the method of Durrelman and Simon (1989) and Harrell (2001, 2009) by placing knots at fixed quantiles of the predictor's distribution. We selected the number of knots by comparing the AIC (Akaike's information criterion) values for the native species models containing different number of knots on the elevation term. The native species model containing three knots had the lowest AIC value and was chosen as the best model. We also added nonlinear terms to the year variable; however, no nonlinear terms were significant in any of the tested models. In order to make direct comparisons with the native species model we constructed an exotic species regression model using the same terms as the best native model (area, year, and restricted cubic spline term with 3 knots). This method allows for direct comparison of predictor responses. In addition, visual inspection of scatter plots confirmed that this technique resulted in reasonable models. We also examined whether there were any patterns between the independent variables that could affect the results of the model (accomplished by calculating variance

Table 1. Full regression models for native, exotic and total species richness as a function of area, year and elevation. Restricted cubic splines with three knots were added to the elevation term. Partial r^2 values are shown for independent variables and adjusted r^2 are shown for full model.

Model Coefficients	Estimate	S.E.	t	P	r^2
Native model					
Log$_{10}$(Area)	0.127074	0.017911	7.095	< 0.001	0.248
Year	0.002756	0.001273	2.166	0.034	0.023
Elevation	0.000411	0.000133	3.098	0.003	0.182
Elevation'	−0.002398	0.000559	−4.287	< 0.001	
Model				< 0.001	0.670
Exotic model					
Log$_{10}$(Area)	0.206300	0.037991	5.431	< 0.001	0.258
Year	0.009197	0.002699	3.407	0.001	0.101
Elevation	0.000362	0.000282	1.285	0.204	0.036
Elevation'	−0.001942	0.001186	−1.637	0.107	
Model				< 0.001	0.415
Total richness model					
Log$_{10}$(Area)	0.132876	0.019311	6.881	< 0.001	0.253
Year	0.003487	0.001372	2.541	0.013	0.034
Elevation	0.000393	0.000143	2.750	0.008	0.161
Elevation'	−0.002310	0.000603	−3.832	< 0.001	
Model				< 0.001	0.643

inflation factors for each model). These values were low (< 1.6) indicating that collinearity was not a substantial problem.

We also tested models that included an interaction term between area and elevation. These models were difficult to interpret because of uneven distribution of flora sizes along the gradient (e.g., no large floras at high elevations). Therefore, we only present results from models without interaction terms. To determine if spatial regression models (i.e., spatial autoregressive) would be appropriate, we tested the ordinary least squares models for spatial dependence using a Moran's I test of model residuals. None of the models displayed significant spatial autocorrelation ($P < 0.05$) indicating that ordinary least squares is appropriate in this case (Table 2). It is important to note that some of our floras do not represent independent observations because of a few cases of spatial overlap or nestedness within the dataset. Lack of independence can increase Type I errors leading to over-generous rejection of null hypotheses. However, use of spatially explicit regression models had little effect on the model coefficients and P-values. Linear regression models were analyzed and visualized using R software version 2.9 (R Development Core Team 2009) using the Design package version 2.2-0 (Harrell 2009). Moran's I test of model residuals were performed using the spdep package version 0.4-34 (Bivand 2009).

Results. AREA AND YEAR. Native and exotic species showed a positive relationship with area and year in the initial model (Table 1). Exotic species showed a steeper slope than native and total richness with area (Fig. 1). In general, total species richness showed a similar response to natives (model coefficients and r^2 values) for all variables tested (Table 1). This is not surprising because on average, 89% of species in our floras are native. For this reason, figures include only comparison of native and exotic models. The area slopes of the native and exotic models are statistically different since the standard errors of the estimates do not overlap (Table 1). The partial r^2 for the area variable was slightly higher for exotic species (Table 1). Both native and exotic species were positively related to year (Table 1). The slope was somewhat higher for exotic species, indicating that more exotic species are added per year. The year slopes for the native and exotic models are statistically different; however, the overall strength of richness by year was weak (Table 1). Partial r^2 values indicate that exotic species were better predicted than native species by the year variable.

ELEVATION. Native species richness showed a hump-shaped pattern along the elevational gradient (Fig. 2). The peak in richness occurred between 500 and 750 m. Elevation explained 18% of the variation in native
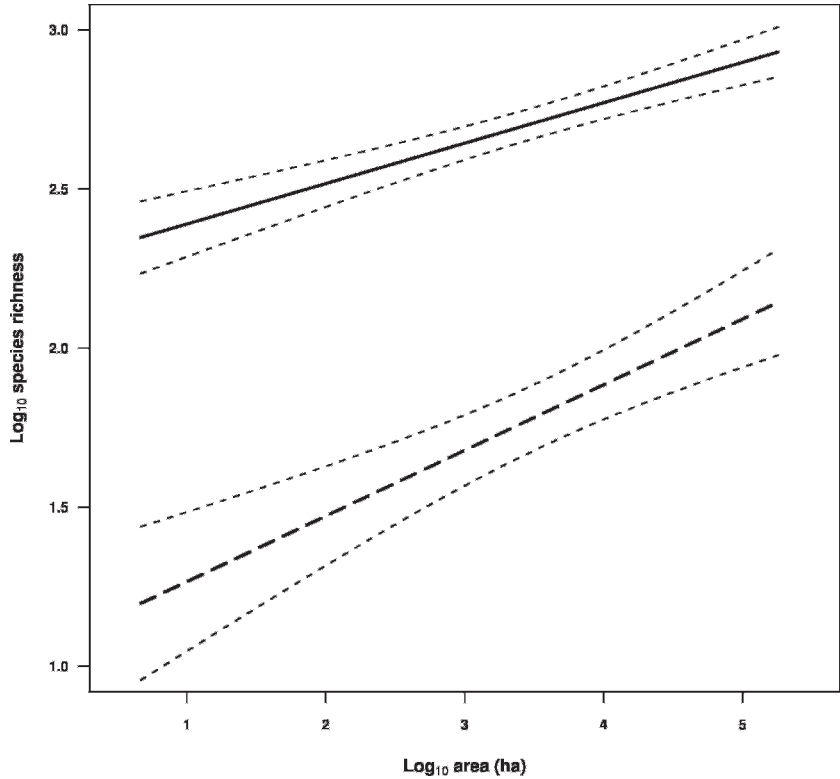
Fig. 1.   Species area relationship for native species (solid line) and exotic species (long dashed line), short dashed lines are 95% confidence intervals for the mean. The prediction lines are based the full regression model including area, year and elevation. The lines indicate $\log_{10}$ species richness for the year 1974 and an elevation of 256.6 meters. Native slope = 0.127, exotic slope = 0.206, see Table 1 for complete regression results.

species richness (Table 1). Elevation was weakly but not significantly related to exotic species richness (Table 1). However, the model did predict a peak in richness at mid-elevations (Fig. 3). The exotic species model differed most notably from the native species model in that richness did not increase or decrease as strongly around the predicted peak in richness (Fig. 3). Exotic richness was consistently low at the highest elevations (above 1500 m). Total species richness (native plus exotic richness) showed a hump-shaped pattern along the elevational gradient (regression coefficients shown in Table 1). This pattern was similar

to the one observed for native species alone and explained 16% of the variation in total species richness. Both native and exotic species richness displayed high variation at the lowest elevations (Fig. 4 and 5). This is particularly true for exotic species richness where there was a high amount of unexplained variation at low elevations (Fig. 5).

Discussion. In this study, native and total species richness showed a hump-shaped pattern along the elevational gradient, similar to those described in Rahbek (2005) and Nogués-Bravo et al. (2008). Exotic species richness

Table 2.   Moran's I test for residual spatial autocorrelation using relative neighbor spatial weights. For explanation of models, see methods section.

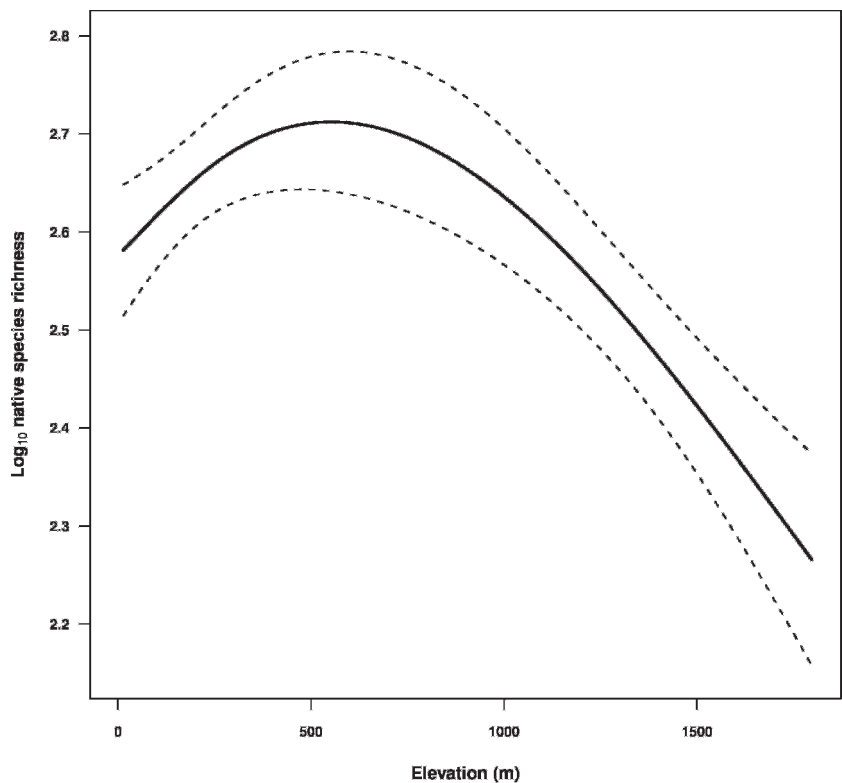| | Moran's I | | | |
	Observed	Expectation	Standard deviate	P
Native species model	−0.0542	−0.0149	−0.3277	0.628
Exotic species model	0.0693	−0.0149	0.7100	0.239
Total richness model	−0.0430	−0.0149	−0.2341	0.593

Fig. 2. Species elevation relationship for native species, short dashed lines are 95% confidence intervals for the mean. The prediction lines are based the full regression model including area, year and elevation. The lines indicate log_{10} species richness for log_{10} area of 3.217 and the year 1974. See Table 1 for complete regression results.

showed a non-significant hump-shaped pattern along the elevation gradient. The exotic richness curve was not as pronounced as that of natives. In addition, in our models elevation did not explain as much of the variation in exotic richness as it did native richness. The few previous studies that have examined exotic richness patterns along elevational gradients have found either a linear decline (Becker et al. 2005, Mallen-Cooper and Pickering, 2008), or a hump-shaped pattern (Tassin and Rivière 2003, Arévalo et al. 2005). Our results are possibly consistent with the latter pattern, but suggest that additional factors influence exotic species richness patterns along the gradient examined in this study.

Despite the lack of a significant elevational effect, exotic species richness was consistently low at elevations above 1500 m. Examination of the model residuals along the elevational gradient indicates values near or below the prediction line at high elevations (Fig. 5). In the Appalachian Mountains, these areas are

characterized by cool, moist summers, and highly variable winters (very cold periods interspersed with warmer rainy periods) with frequent cloud immersion in all seasons. The native plants growing in these areas generally have boreal affinities and the abiotic conditions may limit diversity of both native and exotic species (Alpert et al. 2000). However, propagule pressure is also an important factor that can limit invasion by exotic species at high elevations. For example, when seeds of *Melilotus alba* Desr. were experimentally added to high elevation grasslands in Argentina, emergence was greatest at the highest elevations (Paiaro et al. 2007). This suggests that high elevation areas can be invaded by exotic species if sufficient propagules are introduced, and continued human development at high elevations may lead to a further increase of exotic species over time.

Year was a significant variable in both the native and exotic species models. These results are consistent with those of Palmer (2005),
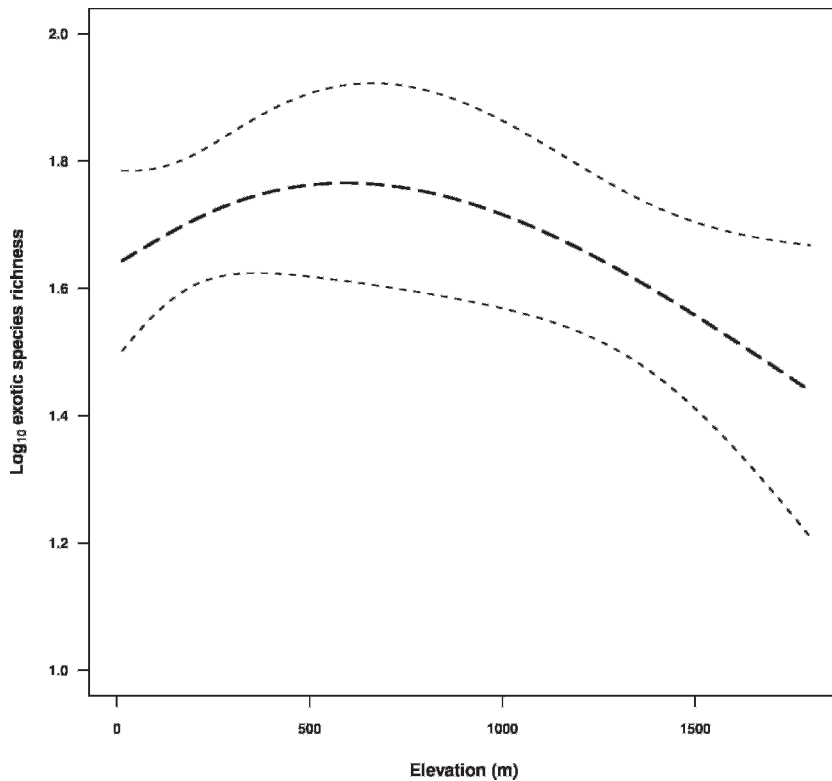
Fig. 3. Species elevation relationship for exotic species, short dashed lines are 95% confidence intervals for the mean. The prediction lines are based the full regression model including area, year and elevation. The lines indicate $\log_{10}$ species richness for $\log_{10}$ area of 3.217 and the year 1974. See Table 1 for complete regression results. Note that elevation was not a significant predictor in the exotic species richness model.

suggesting that when data come from different sources it may be important to account for the effect of year in species richness models. As predicted exotic species richness did increase with time, however native species showed a similar pattern. The number of native species discovered tends to increase with time, perhaps as a result of increased botanical exploration. For example, the number of native species known from North and South Carolina has increase by 290 taxa in the past 40 years, while 432 exotic taxa have been discovered during the same period (Radford et al. 1968, A.S. Weakley, unpublished). Therefore, it may be difficult to distinguish between sampling effects and the detection of novel species introductions.

It is perhaps not surprising that native species richness was more strongly related to elevation than exotic species richness, considering that native and exotic species have not shown consistent richness patterns along environmental gradients elsewhere (Sax and Gaines 2006). For example, Villaseñor and Espinosa-Garcia (2004) found that exotic species showed no species-area relationship for plants in Mexican states. In addition, exotic species do not show the expected species-isolation relationship (decline in richness as distance from mainland increases) commonly found for native species on islands (Sax and Gaines 2006, Blackburn et al. 2007)

The primary mechanisms governing native and exotic species richness patterns along environmental gradients may differ. For example, climatic variables such as temperature and precipitation that vary along elevational gradients may not have the same effects on native and exotic species (McKinney 2002). Historical factors that might influence mass-effects could be less important for exotic species. Although floristic areas (sensu Takhtajan 1986) may have distinct assemblages of exotic taxa (e.g., those present in the Coastal Plain vs. the Blue Ridge), these assemblages
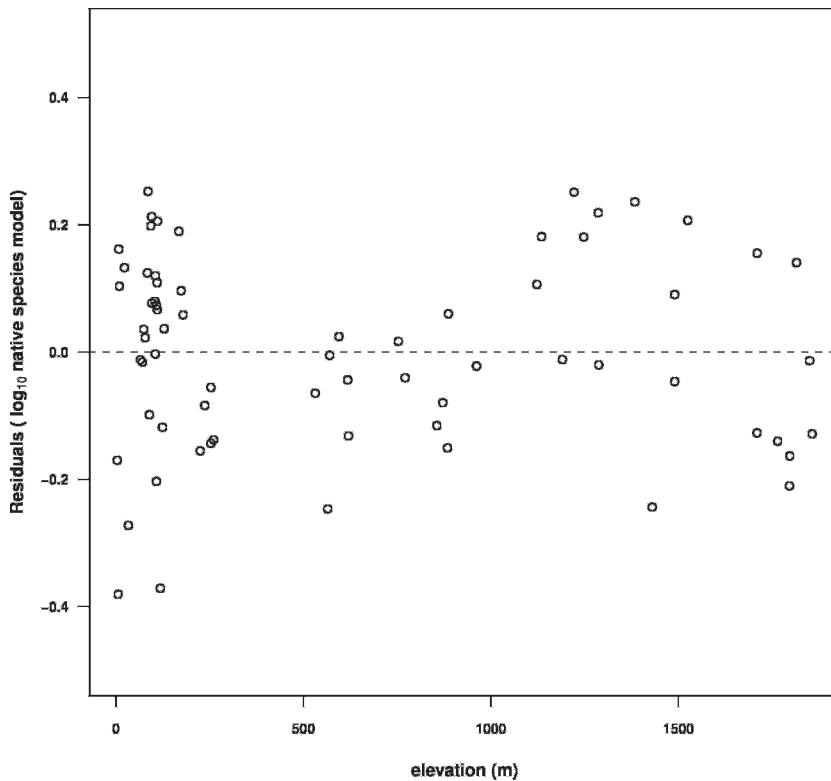
Fig. 4.   Residuals from native species model, including area, year and elevation as independent variables, plotted against elevation.

may not be as pronounced as those of natives. Further, transitions or ecotones may not be as distinct for exotics, leading to a diminished effect of assemblage overlap on richness. Lastly, the growth habit and duration of native and exotic species differ in eastern North America (Fridley 2008). These differing species traits in eastern North America (i.e., overrepresentation of exotic annuals and vines; Fridley 2008) could be an important factor in structuring species assemblages along environmental gradients.

Human influence is an additional factor that changes along elevational gradients and is likely to influence richness patterns. In North Carolina, there is greater human influence at lower elevations, as defined by intensity of human landscape alteration. Specifically at elevations of less than 400 m human landscape alteration (e.g., developed and cultivated land cover types) make up more then 25% of land cover (M.W. Denslow, unpubl. data), and nine of the ten largest cities in North Carolina occur below 400 m elevation (compiled from the U.S. Census Bureau 2000). This could explain some of the high variation in richness for exotic and native species at low elevations in this study (Figs. 4 and 5). In general, human activities have been found to increase species richness (Araújo 2003), yet there is a strong scale effect to this pattern. Pautasso (2007) found that human presence is negatively related to species richness locally (grains $<$ 1 km^2) and positively related at larger scales (grains $>$ 1 km^2). Therefore, human influence should have a positive influence on species richness at the grain and extent of the present study. Further, exotic richness is often strongly correlated with anthropogenic factors such as human population and economic measures (Taylor and Irwin 2004). These human variables (e.g., population) are often stronger predictors than abiotic factors (e.g., climate) of exotic species richness (McKinney 2002). High levels of richness near human population centers have also been associated 'the botanist effect', an artifact of more through sampling near populated areas (Pautasso and McKinney 2007). For these reasons, it seems possible the hump-shaped patterns
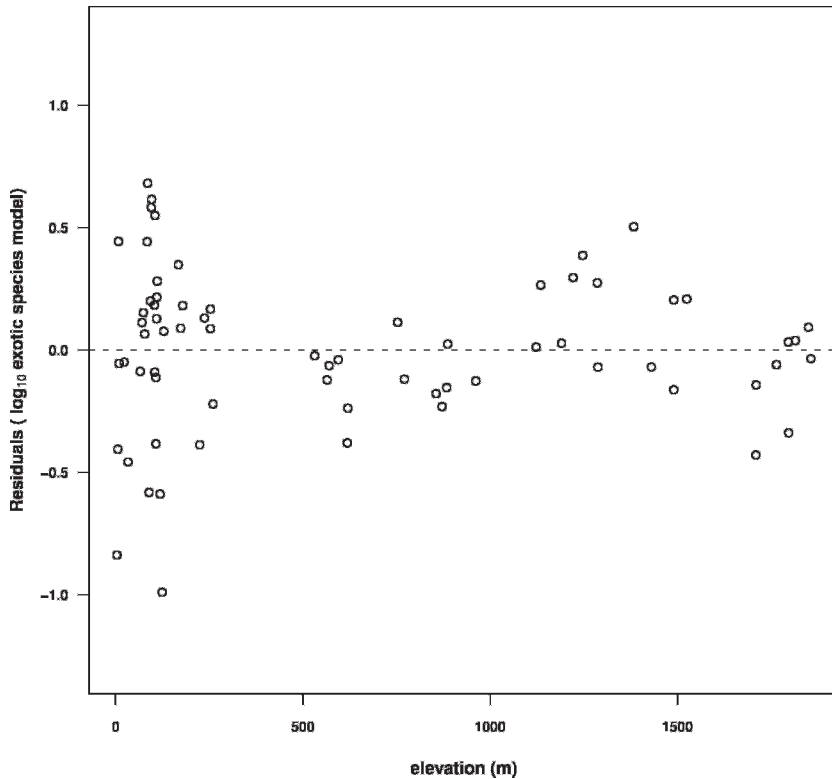
FIG. 5.   Residuals from exotic species model, including area, year and elevation as independent variables, plotted against elevation.

displayed in this study (Figs. 2 and 3) would have been even more pronounced in the absence of a human influence. That is, both native and exotic richness may be enhanced at low elevations due to human activity.

Conclusion. At present, the published literature does not yield a general pattern of exotic richness along elevational gradients. The few studies conducted to date have yielded differing patterns suggesting that exotic richness may in fact be idiosyncratic due to factors such as disturbance history. However, in contrast to our results previous studies have generally found a strong relationship between elevation and exotic richness (e.g., > 50% of variation, Becker et al. 2005, Mallen-Cooper and Pickering 2008). Further, this study contrasts with the results of Palmer (2006) and Mallen-Cooper and Pickering (2008) who found that exotic species richness was more strongly related to elevation than native species richness. Palmer (2006) also found that exotic richness was more predictable than native richness. We found the opposite, with

native richness being more strongly related to physical gradients and better predicted by the regression models. More studies are needed to examine the patterns of native and exotic species in mountain areas.

Literature Cited

ALPERT, P., E. BONE, AND C. HOLZAPFEL. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect. Plant Ecol. Evol. Syst. 3: 52–66.

ARAÚJO, M. B. 2003. The coincidence of people and biodiversity in Europe. Global Ecol. Biogeogr. 12: 5–12.

ARAÚJO, M. B., D. NOGUÉS-BRAVO, J. A. F. DINIZ-FILHO, A. M. HAYWOOD, P. J. VALDES, AND C. RAHBEK. 2008. Quaternary climate changes explain diversity among reptiles and amphibians. Ecography 31: 8–15.

ARÉVALO, J. R., J. D. DELGADO, R. OTTO, A. NARANJO, M. SALAS, AND J. M. FERNÁNDEX-PALACIOS. 2005. Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspect. Plant Ecol. Evol. Syst. 7: 185–202.

ARRHENIUS, O. 1921. Species and area. J. Ecol. 9: 95–99.

BECKER, T., H. DIETZ, R. BILLETER, H. BUSCHMANN, AND P. J. EDWARDS. 2005. Altitudinal distribution of alien plant species in the Swiss Alps. Perspect. Plant Ecol. Evol. Syst. 7: 173–183.

BIVAND, R. 2009. spdep: Spatial dependence: weighting schemes, statistics and models. R package version 0.4-34. <http://cran.r-project.org/web/packages/spdep>

BLACKBURN, T. M., P. CASSEY, AND J. L. LOCKWOOD. 2007. The island biogeography of exotic bird species. Global Ecol. Biogeogr. 17: 246–251.

CRAWLEY, M. J. 1987. What makes a community invasible?, p. 429–453. *In* A. J. Gray, M. J. Crawley, and P. J. Edwards [eds.], Colonization, succession and stability. Blackwell Scientific Publications, Oxford, UK.

DARWIN, C. 1859. On the origin of species. Murrey, London, UK.

DENGLER, J. 2009. Which function describes the species-area relationship best? A review and empirical evaluation. J. Biogeogr. 36: 728–744.

DENSLOW, M. W. 2009. Bibliography, spatial distribution and richness patterns of North Carolina floras. M.S. thesis, Appalachian State University, Boone, NC.

DURRLEMAN, S. AND R. SIMON. 1989. Flexible regression models with cubic splines. Stat. Med. 8: 551–561.

ELTON, C. S. 1958. The ecology of invasions by animals and plants. Methuen & Company Ltd., London, UK. 181 p.

FLORA OF NORTH AMERICA EDITORIAL COMMITTEE. 1993. Flora of North America. Oxford University Press, New York, NY.

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: 3209–3213.

FRIDLEY, J. D., J. J. STACHOWICZ, S. NAEMM, D. F. SAX, E. W. SEABLOOM, M. D. SMITH, T. J. STOHLGREN, D. TILMAN, AND B. VAN HOLLE. 2007. The invasion paradox: reconciling pattern and process in species invasion. Ecology. 88: 3–17.

FRIDLEY, J. D. 2008. Of Asian forests and European fields: eastern U.S. plant invasions in a global floristic context. PLoS ONE. 3: 1–8.

GRYTNES, J. AND C. M. MCCAIN. 2007. Elevational trends in biodiversity, p. 1–8. *In* S. Levin [ed.], Encyclopedia of Biodiversity. Academic Press, San Diego, CA.

GRYTNES, J. A., J. H. BEAMAN, T. S. ROMDAL, AND C. RAHBEK. 2008a. The mid-domain effect matters: simulation analysis of range-size distribution data from Mount Kinabalu, Borneo. J. Biogeogr. 35: 2138–2147.

GRYTNES, J. A., E. HEEGAARD, AND T. S. ROMBAL. 2008b. Can the mass effect explain the mid-altitudinal peak in vascular plant species richness? Basic Appl. Ecol. 9: 373–382.

HARRELL, F. E. 2001. Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis. Springer, New York, NY. 568 p.

HARRELL, F. E. 2009. Design: Design Package. R package version 2.2-0. <http://CRAN.R-project.org/package=Design>

HAWKINS, B. A., J. A. F. DINIZ-FILHO, AND A. E. WEIS. 2005. The mid-domain effect and diversity gradient: Is there anything to learn. Am. Nat. 166: E140–E143.

HULME, P. E. 2008. Contrasting alien and native plant species-area relationships: the importance of spatial grain and extent. Global Ecol. Biogeogr. 17: 641–647.

KIER, G., J. MUTKE, E. DINERSTEIN, T. H. RICKETTS, W. KÜPER, H. KREFT, AND W. BARTHLOTT. 2005. Global patterns of plant diversity and floristic knowledge. J. Biogeogr. 32: 1107–1116.

KÖRNER, C. 2007. The use of 'altitude' in ecological research. Trends Ecol. Evol. 22: 569–574.

KREFT, H., W. JETZ, J. MUTKE, G. KIER, AND W. BARTHLOTT. 2007. Global diversity of island floras from a macroecological perspective. Ecol. Lett. 11: 116–127.

LOBO, J. M., A. BASELGA, J. HORTAL, A. JIMÉNEZ-VALVERDE, AND J. F. GÒMEZ. 2007. How does the knowledge of Iberian dung beetle species accumulate over time? Divers. Distrib. 13: 772–780.

LOMOLINO, M. V. 2001. Elevational gradients of species-density: historical and prospective views. Global Ecol. Biogeogr. 10: 3–13.

MACARTHUR, R. H. AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ. 203 p.

MACK, R. N. AND M. ERNEBERG. 2002. The United States naturalized flora: largely the product of deliberate introductions. Ann. Mo. Bot. Gard. 89: 176–189.

MALLEN-COOPER, J. AND C. M. PICKERING. 2008. Linear declines in exotic and native plant species richness along an increasing altitudinal gradient in the Snowy Mountains, Australia. Austral. Ecol. 33: 684–690.

MCCAIN, C. M. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. Global Ecol. Biogeogr. 16: 1–13.

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. Divers. Distrib. 8: 311–318.

MITTELBACH, G. C., D. W. SCHEMSKE, H. V. CORNELL, A. P. ALLEN, J. M. BROWN, M. B. BUSH, S. P. HARRISON, A. H. HURLBERT, N. KNOWLTON, H. A. LESSIOS, C. M. MCCAIN, A. R. MCCUNE, L. A. MCDADE, M. A. MCPEEK, T. J. NEAR, T. D. PRICE, R. E. RICKLEFS, K. ROY, D. F. SAX, D. SCHLUTER, J. M. SOBEL, AND M. TURELLI. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol. Lett. 10: 315–331.

NOGUÉS-BRAVO, D., M. B. ARAÚJO, T. ROMDAL, AND C. RAHBEK. 2008. Scale effects and human impact on the elevational species richness gradients. Nature. 453: 216–220.

PAIARO, V., A. MANGEAUD, AND E. PUCHETA. 2007. Alien seedling recruitment as a response to altitude and soil disturbance in the mountain grasslands of central Argentina. Plant Ecol. 193: 279–291.

PALMER, M. W. 1995. How should one count species? Nat. Areas J. 15: 124–135.

PALMER, M. W. 2005. Temporal trends of exotic species richness in North American floras: An overview. Ecoscience 12: 386–390.

PALMER, M. W. 2006. Scale dependence of native and alien species richness in North American floras. Preslia 78: 427–436.

PALMER, M. W. 2007. Species-area curves and the geometry of nature, p. 15–31. *In* D. Stoch, P. A. Marquest, and J. H. Brown [eds.], Scaling biodiversity. Cambridge University Press, Cambridge, UK.

PAUTASSO, M. 2007. Scale dependence of the correlation between human population presence and vertebrate and plant species richness. Ecol. Lett. 10: 16–24.

PAUTASSO, M. AND M. L. MCKINNEY. 2007. The botanist effect revisited: plant species richness, county area, and human population size in the United States. Conserv. Biol. 21: 1333–1340.

QIAN, H. 2009. Beta diversity in relation to dispersal ability for vascular plants in North America. Global Ecol. Biogeogr. 18: 327–332.

R DEVELOPMENT CORE TEAM. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>

RADFORD, A., H. AHLES, AND C. BELL. 1968. Manual of the vascular flora of the Carolinas. The University of North Carolina Press, Chapel Hill, NC. 1183 p.

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 University Press, Cambridge, UK. 436 p.

SANDERS, N. J., J. LESSARD, M. C. FITZPATRICK, AND R. R. DUNN. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecol. Biogeogr. 16: 640–649.

SAX, D. F. 2001. Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. J. Biogeogr. 28: 139–150.

SAX, D. F. AND S. D. GAINES. 2006. The biogeography of naturalized species and the species-area relationship: reciprocal insights to biogeography and invasion biology, p. 449–480. *In* M. W. Cadotte, S. M. McMahon, and T. Fumaki [eds.], Conceptual ecology and invasions biology: reciprocal approaches to nature. Springer, Berlin, FRG.

SAX, D. F., J. J. STACHOWICZ, J. H. BROWN, J. F. BRUNO, M. N. DAWSON, S. D. GAINES, R. K. GROSBERG, A. HASTINGS, R. D. HOLT, M. M. MAYFIELD, M. I. O'CONNOR, AND W. R. RICE. 2007. Ecological and evolutionary insights from species invasions. Trends Ecol. Evol. 22: 465–471.

STOHLGREN, T. J., D. BARNETT, C. FLATHER, J. KARTESZ, AND B. PETERJOHN. 2005. Plant species invasions along the latitudinal gradient in the United States. Ecology. 86: 2298–2309.

STOHLGREN, T. J., C. JARNEVICH, G. W. CHONG, AND P. H. EVANGELISTA. 2006. Scale and plant invasions: a theory of biotic acceptance. Preslia 78: 405–426.

TAKHTAJAN, A. 1986. Floristic regions of the world. University of California Press, Berkeley, CA. 522 p.

TASSIN, J. AND J. RIVIÈRE. 2003. Species richness altitudinal gradient of invasive plants on Reunion Island (Mascareigne archipelago, Indian Ocean). Revue D'Écologie–La Terre et la Vie 58: 257–270.

TAYLOR, B. W. AND R. E. IRWIN. 2004. Linking economic activities to the distribution of exotic plants. Proc. Natl. Acad. Sci. USA. 101: 17725–17730.

U.S. CENSUS BUREAU. 2000. State and county Quickfacts: North Carolina. <http://quickfacts.census.gov>

USDA-NRCS. 2008. The PLANTS database, National Plant Data Center, Baton Rouge. <http://plants.usda.gov>

VILLASEÑOR, J. L. AND F. J. ESPINOSA-GARCIA. 2004. The alien flowering plants of Mexico. Divers. Distrib. 10: 113–123.

WEAKLEY, A. S. 2008. Flora of the Carolinas, Virginia, Georgia, northern Florida and surrounding areas. working draft of 7 April 2008. http://www.herbarium.unc.edu/flora.ht

Appendix A

Table of taxonomic concept comparisons. Richness counts at the level of species for two different taxonomic concepts. See Appendix B for complete flora citation information.

Flora Citation	Species based on Radford et al. (1968)	Species based on Weakley (2008)	% diff.
Tucker 1972	677	693	**2.3**
Pittillo and Lee 1984	596	590	**1**
Bradshaw 1987	430	426	**0.9**
Michael 1969	328	327	**0.3**
Rohrer 1983	355	353	**0.6**
Mean			**1**

Appendix B.

Complete citation information of the floras used in this study. Note that some citations include more than one flora site.

BEARD, L. S. 1958. A floristic study along the Lower Deep River of North Carolina. M.A. thesis, University of North Carolina, Chapel Hill, North Carolina.

BLAIR, A. E. 1967. Vascular Flora of Beaufort County, North Carolina. M.S. thesis, North Carolina State University at Raleigh.

BRADSHAW, T. L. 1987. Floristic survey and vegetational analysis of Lost Cove, Avery County, North Carolina. M.S. thesis, North Carolina State University, Raleigh, North Carolina.

BRUTON, V. C. 1968. Floristic survey and vegetational analysis of Cliffs of the Neuse State Park in North Carolina. M.S. thesis, North Carolina State University, Raleigh, North Carolina.

BURK, C. J. 1959. A floristic study of a Sandhill Area on the North Carolina Coastal Plain. M.A. thesis, University of North Carolina, Chapel Hill, North Carolina.

CORDA, S. L. 1982. The flora and community types of Goose Creek State Park, North Carolina. M.S. thesis, North Carolina State University, Raleigh, North Carolina.

DuMOND, D. M. 1970. Floristic and vegetational survey of the Chattooga River Gorge. Castanea 35: 201–244.

FEIL, E. G. 1987. Floristics and vegetation of Chimney Rock Park, Rutherford County, North Carolina. M.S. thesis, University of North Carolina, Charlotte, North Carolina.

FLOYD, J. W. 1996. The vascular flora of Medoc Mountain State Park. Halifax County, North Carolina. J. Elisha Mitchell Sci. Soc. 112: 45–72.

GUPTON, O. W. 1960. A vascular flora of the North Carolina Sandhills Wildlife Management Area. M.A. thesis, University of North Carolina, Chapel Hill, North Carolina.

HOFFMAN, H. L. 1964. Check list of vascular plants of the Great Smoky Mountains. Castanea 29: 1–45.

HORTON, J. H. 1957. A vascular flora of Rowan County, North Carolina. M.A. thesis, University of North Carolina, Chapel Hill, North Carolina.

HOUCK, D. F. 1956. Flood plain flora of the Deep River Triassic Basin. M.A. thesis, University of North Carolina, Chapel Hill, North Carolina.

JOHNSON, F., J. ESTES, R. RUDMAN, R. THOMPSON, P. MORRELL, G. SCHNELL, AND D. GEORGE. 1991. Floral inventory of Fort Bragg, North Carolina. Final Report to U.S. Army Construction Engineering Research Laboratory, Champaign, Illinois, Oklahoma Biological Survey, University of Oklahoma, Norman, Oklahoma.

JONES, S. I. 1971. Floristic survey and vegetational analysis of Yates Pond Biological Area in Wake County, North Carolina. M.S. thesis, North Carolina State University, Raleigh, North Carolina.

JONES, T. H. 1973. Floristic survey and vegetational analysis of Raven Rock State Park, Harnett County, North Carolina. M.S. thesis, North Carolina State University, Raleigh, North Carolina.

KEARNEY, T. H. 1901. Report on a botanical survey of the Dismal Swamp Region. Contr. U.S. Natl. Herb. 5: 321–550.

KENNEMORE, D. E. 1995. Floristics of the Kings Mountain National Military Park and the Kings Mountain State Park. M.S. thesis, University of South Carolina, Columbia, South Carolina.

KESSLER, P. A. 1956. A floristic study of the Triassic sediments, Deep River coal field, North Carolina. M.A. thesis, University of North Carolina, Chapel Hill, North Carolina.

KRINGS, A. AND C. FRANKLIN. 2004. An annotated, preliminary checklist of the vascular flora of Camp Butner, North Carolina. Sida 21: 1131–1139.

LACEY, V. H. 1979. A floristic survey of Phoenix Mountain, Ashe County, North Carolina: a thesis. M.A. thesis, Appalachian State University, Boone, North Carolina.

LARKE, J. O. 1991. Checklist of the vascular plants of the Hunt Arboretum and Gray Bluff Garden: including tables on the taxonomic composition of the flora, largest plant families, summary of the flora, noteworthy plants, and plants occurring on adjacent lands. North Carolina Botanical Garden, Chapel Hill, N.C.

McCORMICK, C. A. AND P. S. WHITE. 1993. Conservation project: the nature trail area, Coker Pinetum, and Stillhouse Bottom Nature Preserve: final report. Page 450. North Carolina Botanical Garden, University of North Carolina, Chapel Hill, North Carolina.

McLEOD, D. E. 1988. Vegetation patterns, floristics and environmental relationships in the Black and Craggy Mountains of North Carolina. Ph.D. dissertation, University of North Carolina at Chapel Hill.

McNEELY, J. A. 1960. A floristic ftudy of the Lake Norman Area in Iredell and Catawba Counties. M.S. thesis, University of North Carolina, Chapel Hill, North Carolina.

MEMMINGER, E. R. 1915. A list of plants growing spontaneously in Henderson County, NC. J. Elisha Mitchell Sci. Soc. 31: 126–149.

MICHAEL, J. L. 1969. The vascular flora of Bullhead Mountain, Alleghany County, North Carolina. M.S. thesis, University of North Carolina, Chapel Hill, North Carolina.

MORGAN, J. T. 1962. A Vascular Flora of Morrow Mountain State Park, Stanly County, North Carolina. M.A. thesis, University of North Carolina, Chapel Hill, North Carolina.

MUSSELMAN, L. J., D. L. NICKRENT, AND G. F. LEVY. 1977. A contribution towards a vascular flora of the Great Dismal Swamp [Virginia, North Carolina]. Rhodora 79: 240–268.

PALMER, M. W. 1990. Vascular flora of the Duke Forest, North Carolina. Castanea 55: 229–244.

PITTILLO, J. D. AND M. LEE. 1984. Reference plant collection of the Coweeta Hydrologic Laboratory. General Technical Report, United States Department of Agriculture, Forest Service,

Southeastern Forest Experiment Station, Asheville, North Carolina.

POINDEXTER, D. B. 2006. Vascular flora of Mount Jefferson State Natural Area and environs, Ashe County, North Carolina: a thesis. M.S. thesis, Appalachian State University, Boone, North Carolina.

PULTORAK, R. W. 1969. Vascular flora of northern Wake County, North Carolina. M.S. thesis, North Carolina State University, Raleigh, North Carolina.

RAMSEUR, G. S. 1960. The vascular flora of high mountain communities of the Southern Appalachians. J. Elisha Mitchell Sci. Soc. 76: 82–112.

RODGERS, C. L. 1969. Vascular plants in Horsepasture Gorge. Castanea 34: 374–394.

RODGERS, C. L. AND R. F. SHAKE. 1965. Survey of vascular plants in Bearcamp Creek watershed. Castanea 30: 149–166.

RODGERS, C. L. AND G. W. SHIFLET. 1978. Plants of the Eastatoe. South Carolina Museum Commission, Museum Bulletin 2: 1–20.

ROHRER, J. R. 1983. Vegetation pattern and rock type in the flora of the Hanging Rock Area, North Carolina. Castanea 48: 189–205.

RUSSO, M. J., B. A. SORRIE, B. VAN EERDEN, AND P. E. HIPPENSTEEL. 1993. Rare and endangered plant survey and Natural Area inventory for Fort Bragg and Camp Mackall Military Reservations, North Carolina. Nature Conservancy and North Carolina Natural Heritage Program, Carrboro, North Carolina.

SAWYER, G. P. 1968. The vascular flora of William B. Umstead State Park, Wake County, North Carolina. M.A. thesis, University of North Carolina, Chapel Hill, North Carolina.

SKEAN, J. D. 1982. The vascular flora and plant community types of Durant Nature Park, Wake County, North Carolina. M.S. thesis, North Carolina State University. Raleigh, North Carolina.

SMITH, E. L. V. 1977. Floristic survey and vegetational analysis of the South Mountains State Park, Burke County, North Carolina. M.S. thesis, North Carolina State University, Raleigh, North Carolina.

SORRIE, B. A., J. B. GRAY, AND P. J. CRUTCHFIELD. 2006. The vascular flora of the Longleaf Pine ecosystem of Fort Bragg and Weymouth Woods, North Carolina. Castanea 71: 129–161.

STRATTON, D. AND P. S. WHITE. 1982. Grassy balds of Great Smoky Mountains National Park: vascular plant floristics, rare plant distributions, and an assessment of the floristic data base. Page 33. Research/Resources Management Report, United States Department of the Interior, National Park Service, Atlanta, Georgia.

SWAB, E. C. 1990. The flora and vegetation of White Pines Natural Area, Chatham County, North Carolina. M.S. thesis, North Carolina State University, Raleigh, North Carolina.

TAGGART, J. B. 1973. Floristic survey and vegetational analysis of Stone Mountain State Park in North Carolina. M.S. thesis, North Carolina State University, Raleigh, North Carolina.

TAYLOR, T. D. 1974. A check list of vascular flora of Tablerock Mountain, Burke County, North Carolina: a thesis. M.S. thesis, Appalachian State University, Boone, North Carolina.

TUCKER, G. E. 1972. The vascular flora of Bluff Mountain, Ashe County, North Carolina. Castanea 37: 2–26.

WARE, D. M. E. 1973. Floristic survey of the Thompson River watershed. Castanea 38: 349–378.

WELLS, E. F. 1970. A vascular flora of the Uwharrie Wildlife Management Area, Montgomery County, North Carolina. M.A. Thesis, University of North Carolina, Chapel Hill, North Carolina.

WHITE, P. S. 1982. The flora of Great Smoky Mountains National Park: an annotated checklist of the vascular plants and a review of previous floristic work. United States Department of Interior, National Park Service, Washington, D.C.

WHITE, P. S., R. T. BUSING, AND J. O. LARKE. 1992. Conservation project: the Mason Farm Biological Reserve: final report. North Carolina Botanical Garden, University of North Carolina, Chapel Hill, North Carolina.

WHITE, R. D. 2003. Vascular plant inventory and plant community classification for Carl Sandburg Home National Historic Site. Nature Serve: Durham, North Carolina.

WHITE, R. D. AND M. PAYNE. 2003. Vascular plant inventory and plant community classification for Guilford Courthouse Military Park. Nature Serve: Durham, North Carolina.

WICHMANN, B. L., L. ALLÄ, AND P. S. WHITE. 2000. Conservation project: the Laurel Hill Nature Preserve and ''Billy Hunt's Garden'' with an update on the rare species and exotic species of the Hunt Arboreturm, Gray Bluff Garden, and the Mason Farm Biological Reserve: final report. North Carolina Botanical Garden, University of North Carolina, Chapel Hill, North Carolina.