BIBLIOGRAPHY, SPATIAL DISTRIBUTION AND RICHNESS PATTERNS OF NORTH
CAROLINA FLORAS

A Thesis

by

MICHAEL WARD DENSLOW

Submitted to the Graduate School

Appalachian State University

in partial fulfillment of the requirements for the degree of
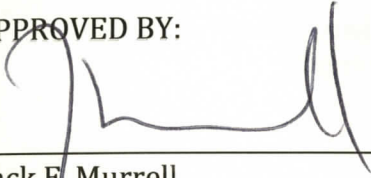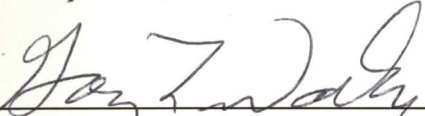
MASTER OF SCIENCE

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Department of Biology

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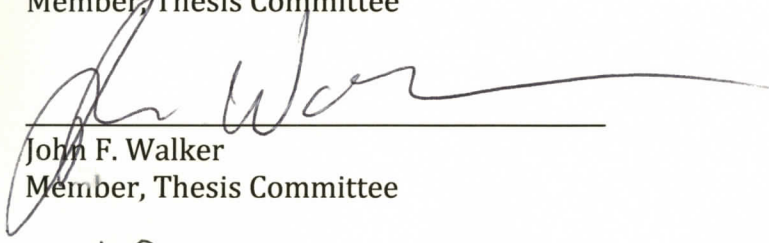By
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December 2009

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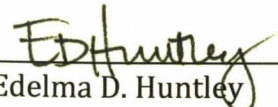Gary L. Walker
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FOREWARD

This thesis is presented in three separate chapters, with a general introduction presented at the beginning of the document. Each individual chapter is written as a stand-alone publication, with a self-contained literature review and bibliography. This format was chosen because three relatively distinct studies were completed for this thesis project and presenting them separately increased the readability of the thesis. Further, this format facilitates submission for publication, as each chapter will be submitted separately for publication. The chapters are formatted in the style of the Journal of the Torrey Botanical Society.

ABSTRACT

BIBLIOGRAPHY, SPATIAL DISTRIBUTION AND RICHNESS PATTERNS OF NORTH
CAROLINA FLORAS

(December 2009)

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This thesis utilizes primary biodiversity literature to answer questions related to macroecology and the spatial patterns of floristic exploration. Vascular plant checklists (floras) supply key information for biodiversity studies by providing a comprehensive picture of the floristic composition of a specific study area. A bibliography of floras conducted within the state of North Carolina was assembled. Eighty-six floras were completed within North Carolina between the years 1834 and 2009. Floras conducted in North Carolina cover areas of varying size, from small islands and state parks to entire counties. These studies include journal articles, government publications, technical reports and Master's theses. More than half of the flora citations were not published in scientific journals and were often difficult to discover or obtain.

The spatial patterns of botanical knowledge have strong implications for conservation planning, as well as for macroecological and biogeographic studies.

However, many areas worldwide are still in need of baseline botanical information. In a time when biodiversity information is so critical, we must utilize resources efficiently to obtain missing data on the floristic composition of local areas and the geographic distributions of plant taxa. This study examined (1) the geographical survey gaps in botanical exploration and (2) the spatial distribution of published North Carolina local floras. For 86 North Carolina floras, study locations and spatial extents were mapped and the spatial patterns were analyzed. A site selection simulation was conducted to assess whether the flora sites were significantly clustered around North Carolina herbaria. Significant botanical survey gaps were identified, suggesting that some areas within North Carolina remain inadequately explored botanically. These areas were highlighted to encourage exploration by future investigators. Floras were clustered around North Carolina herbaria. These insights will help future botanists efficiently plan for future expeditions into botanically little-known areas.

Floristic studies from North Carolina were used to compare the patterns of total, native and exotic plant species richness along an elevation gradient from sea level (Atlantic coast) to the summits 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. The effects of size of study area, year of study, and elevation on species richness were modeled using a dataset of 68 floristic studies. Both 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. Elevation was not a significant variable in the exotic species richness model. This contrasts with the few

previous studies that have examined exotic richness patterns along elevational gradients, which have found either a linear decline or a humped shaped pattern. Both native and exotic species showed high variation in richness at elevations below 400 m. It is concluded that different processes may govern native and exotic plant richness patterns. Exotic richness patterns along gradients may in fact be idiosyncratic due to factors such as disturbance history.

ACKNOWLEDGEMENTS

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THESIS INTRODUCTION

Access to adequate primary biodiversity information is critically important to address current issues affecting society (Costello 2009). Rapid changes are taking place globally that are leading to increased species extinction and imperilment. In recent years there has been greater interest in mobilizing various forms of data to understand the changes that are taking place or to predict how species will change in the future (Penev et al. 2009, Steiniger and Hay 2009). Large scale and local databases are making this information increasingly accessible to scientists worldwide.

There are two primary forms of biodiversity data: data that have been recently collected, processed and made available electronically and legacy data that was collected in the past and is not currently available in digital form. Biodiversity Information Standards (TDWG) is a global initiative that focuses on ways to efficiently exchange biological data. Technological advances are assisting in the enhanced discovery and retrieval of this information (Penev et al. 2009). However major challenges still exist when dealing with the mobilization of legacy data that is not yet in a digital format.

The principal form of biodiversity data is museum specimens and their associated data (e.g., identifications, georeference and habitat specifics). However, there are many forms of data that are used in the analysis and description of the earth's species. For example, ecological plot data and gene sequences are also extensively used and many initiatives focus on the curation and discovery of these data sets (VegBank and GenBank). In addition,

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scientific literature can be parsed in order to extract biodiversity data, either by humans, information retrieval algorithms or a combination of both. In the case of the Biodiversity Heritage Library, taxonomic literature is identified by humans and digitized with optical character recognition (OCR) software. This literature can then be searched so that relevant articles can be identified. More recently, algorithms are being tested to parse out species names that occur within publications. However these algorithms are still in their infancy and much manual work is still needed to make use of biological literature to its fullest extent.

This thesis utilizes literature in the form of vascular plant checklists (floras) to answers questions related to Macroecology and the spatial patterns of floristic exploration. The analyses are focused on the state of North Carolina, but the methods used here could be usefully applied to other states and regions. Floras have been successfully used to answer a variety of questions in large-scale biodiversity research (Kreft et al. 2007, McLaughlin 2007, Qian et al. 2007). Floras can provide important insights into species patterns over time and space. Global and regional data sharing initiatives such as the Global Biodiversity Information Facility (GBIF) and Southeast Regional Network of Expertise and Collections (SERNEC) are actively pursuing ways to incorporated literature into their data portals.

This study identified a significant factor in the use of literature in biodiversity analyses. More than half of the flora citations used in this thesis were not published in scientific journals. Instead these studies were in the forms of Master's theses and technical reports. These forms of literature are often not discovered using commercial databases such as those used by many libraries. For this reason it is especially important to utilize the expertise of regional and local networks of experts to discover these important resources.

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Chapter 1: A bibliography of North Carolina local floras

The objective of this paper is to provide a list of floras conducted within the state of North Carolina. North Carolina has a long history of botanical exploration and subsequent publication (e.g., Croom 1837, Curtis 1867, Chapman 1883, Small and Heller 1892, Small 1933, Radford et al. 1968, Weakley 2008). In fact, the oldest herbarium in the United States, Salem College founded in 1820, is located within the state (Thiers 2009). Compilations of botanical literature for a specific geographic area can be extremely valuable to the botanical community (Bates 1985, Jones et al. 2007, Palmer 2007). Several publications have provided botanical bibliographic information relevant to the state of North Carolina (Egler 1961, Hardin and DuMond 1971, DeYoung et al. 1982 , Wofford and White 1981, White 1982, Matthews and Mellichamp 1989, Burk 2006, Weakley 2008). However, only one of these publications focused specifically on the state (Hardin and DuMond 1971). Hardin and DuMond (1971) listed numerous publications relevant to the identification of the plants (including fungi, bryophytes and algae) and few floras (vascular plant checklists) were included. Floras provide valuable information for broad-scale biodiversity analyses (Palmer 2005, Kreft et al. 2007, Qian et al. 2007). In addition, they provide an important reference for botanists and ecologists in the field.

Materials and Methods. The first step in procuring the floras was to define my criteria for inclusion. For the purposes of this bibliography, a flora is a list of plants for a

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given area (sensu, Lawrence 1951, Palmer et al. 1995). The author of the flora must have intended for the list to be complete. Despite containing the word flora in the title, some publications were not intended by the author to be complete checklists (e.g., Craigmile 1922, McCurdy 1975, Wyatt and Fowler 1977), and such publications were excluded from this bibliography. If a list was restricted taxonomically (e.g., Poaceae excluded), or seasonally (e.g., spring flora, Glasson 1934, Palmer 1970) it was also excluded from the present list. Finally, the area circumscribed must be unambiguous and the study location should be clearly stated.

If the area in terms of size and geographic location are not clearly stated it can severely limit the usefulness of a flora for two reasons. First, the number of species in a given list is strongly determined by its size (Rosensweig, 1995). For this reason, comparative research is difficult without an accurate area measurement (e.g., in hectares). The area covered by a flora allows for the evaluation of its biodiversity as compared with other areas. Second, detailed geographic location is also critical to the evaluation of a flora. If the exact geographic boundaries are not known, this limits the use of the species list for assessing specific species distributions, range extensions and importance of occurrences. Furthermore, it can be difficult to add supplementary information for further floristic analysis. For example, if the elevational range for the site is not clearly stated by the author it can be impossible to assess this without a clear map or explanation of study area boundaries. A few floras were found that had unclear study area boundaries and were therefore excluded from the bibliography (e.g., Croom 1837, Sears 1967). Palmer et al. (1995) examined in detail the data that should be included in floras. In order to enhance the value of future floristic studies floristicians are encouraged to closely follow the standards outlined in that paper.

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Literature citations were obtained from a number of different sources. For example, a large number of citations were initially 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 about the FloraS of North America project can be found in Palmer (2005) and at http://botany.okstate.edu/floras/. Additional floras were obtained from standard literature searches (e.g., Agricola), bibliographies of known floras, journal scanning (e.g., Castanea, Journal of the Elisha Mitchell Scientific Society) and personal communications. In addition, I searched the library catalogs of all North Carolina colleges and universities in order to locate unpublished thesis and dissertations. This method was found to be more reliable than searching the Dissertation Abstracts database. Floras were obtained in hard copy through electronic download or Interlibrary Loan. Each publication was reviewed to make sure it fit the criteria listed above. Often they did not, and the reason for exclusion was noted. The full list of publications reviewed for this study is available upon request. In general, only one citation for each flora is listed in the bibliography. For example, if a thesis was conducted and then the same research was published in a journal, the most recent citation was used.

Results. Approximately 200 citations were examined for this study. From these examined citations, 86 floras were identified that met all the criteria for inclusion in the bibliography (Appendix A). In some rare cases floras were published in sections and therefore have more then one citation associated with them (e.g., Peattie 1928, 1929a, 1929b, 1929c, 1930, 1931, 1937 in Appendix A). The floras ranged in publication date from 1834-2009 (Fig. 1). There was a conspicuous increase in the number of floras beginning in the

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1950s (Fig. 1). This work was largely conducted by A.E. Radford students at the University of North Carolina, Chapel Hill (Burk 2006) and J.W. Hardin students at North Carolina State University. Twenty-eight North Carolina floras were published in scientific journals such as Castanea and The Journal of the Elisha Mitchell Scientific Society. The remaining floras appeared in less widely distributed forms such as government documents (17), theses/dissertations (37) and unpublished manuscripts (4). The floras were distributed across the state of North Carolina with 37 (43%) conducted in the coastal plain, 26 (30%) in the mountains and 23 (27%) in the piedmont. The study sites of each flora fell into 5 categories: counties, military lands, mixed ownership, preserve/parks and entirely private properties (Fig. 2). Not surprisingly there appears to be a strong preference for studies within preserves and parks (e.g., state parks and natural areas).
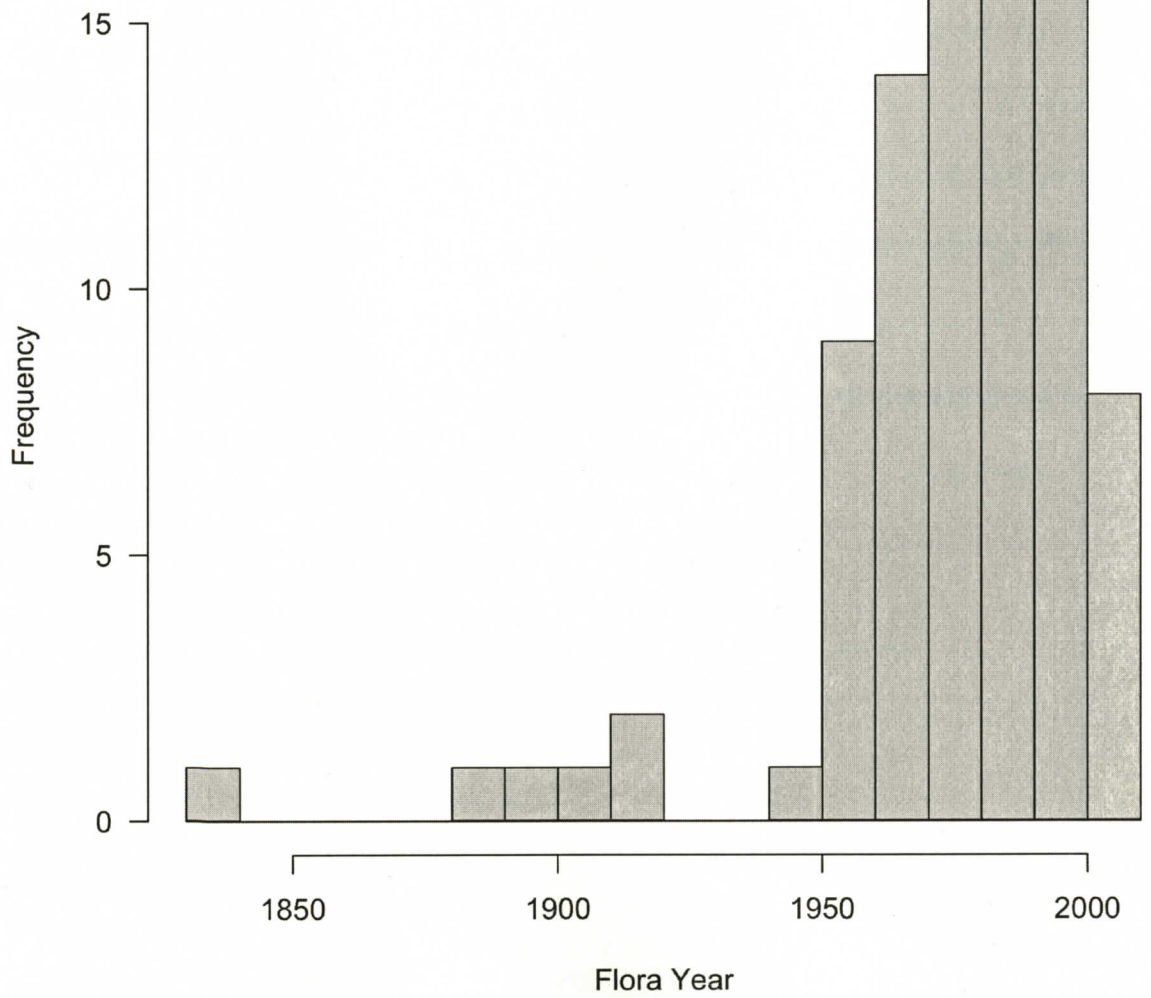
Fig. 1. Histogram showing the years that North Carolina floras were published.
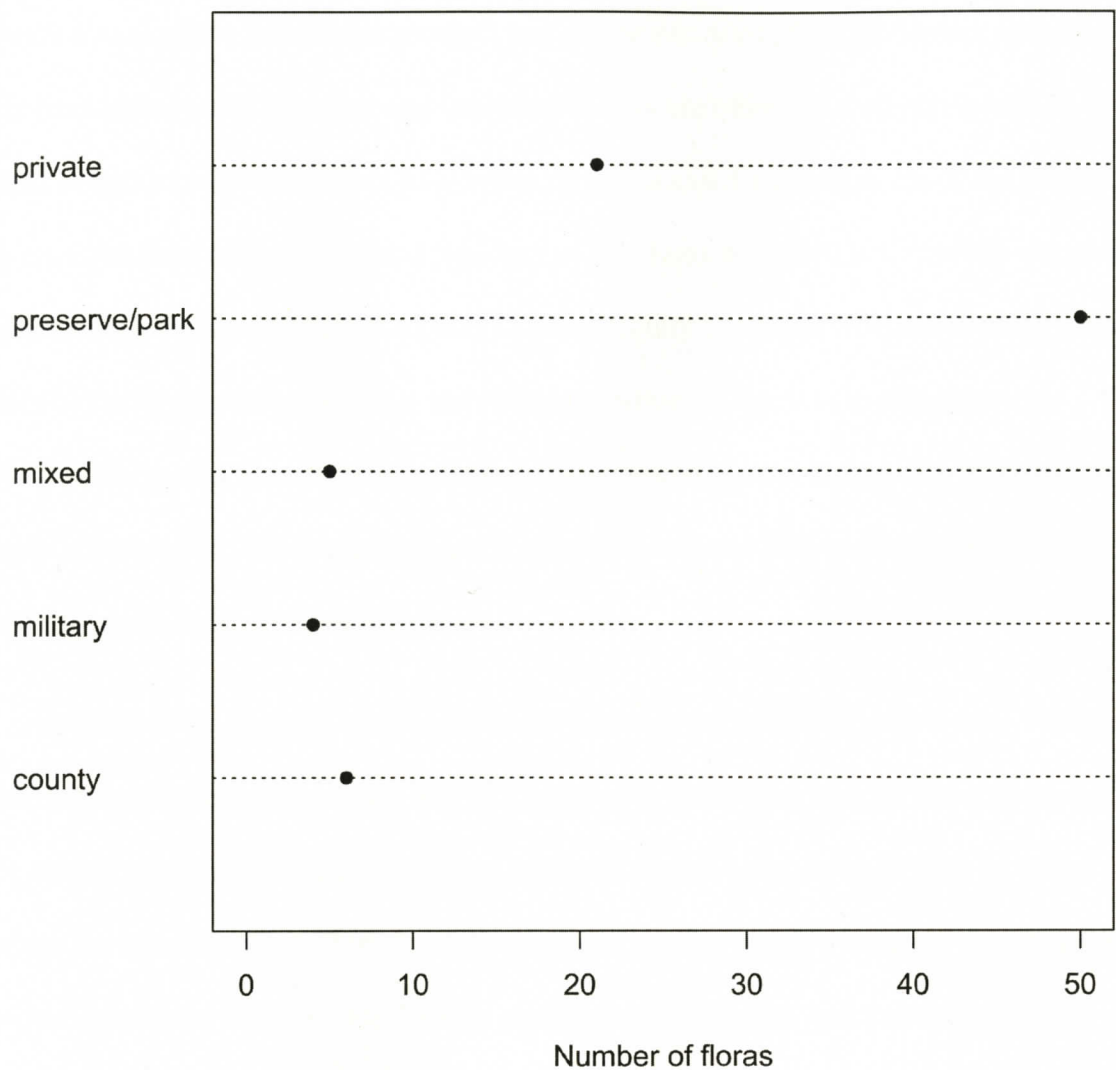
Fig. 2. Dotchart displaying the number of flora conducted in each of the different study site categories in North Carolina.

Discussion. The bibliography presented here is presumed to be relatively complete. This statement is based on the observation that after exhaustive searching, the databases, literature sources and personal communications ceased to yield new citations. However, it is difficult to accurately measure the completeness of the presented bibliography. New floras

will undoubtedly be added to this list. For example, older floras (prior to 1930's) can be obscure and difficult to obtain. In addition, some floras have vague names (i.e., title does not suggest that a complete plant list is present) and can be easily overlooked. Lastly, technical reports from government agencies and unpublished lists are often not well publicized. In addition, in many cases only one or two copies of theses and dissertations exist, and are not easily obtained from some libraries. A majority of the floras identified in this study are grey literature, which can be difficult to access. The community can assist with this bibliographic research by reviewing the present list and bringing additional floras to my attention. In addition, an electronic file containing all citations reviewed but not included in this study is available upon request. These citations are not floras as defined here and are being made available to avoid duplication of efforts.

Floristic bibliographies can be extremely useful to the botanical community. Floras can provide researchers with a plant list for a given area facilitating species identification. Future workers can also look at areas where previous studies have not been done to target new areas for investigations. Floristic bibliographies can also provide locations for sites that can be resampled and analyzed for floristic change (e.g., Harrelson and Cantino, 2006). While many floras have been conducted in North Carolina, there are still many areas in need of investigation. This effort seems especially urgent in light of climate and land-use change taking place in our area (Mearnes et al. 2003, Turner et al. 2003).

The biodiversity informatics community has recognized the need to integrate literature sources as data into global databases. Efforts such as the Global Biodiversity Information Facility (http://www.gbif.org/) and the Biodiversity Heritage Library (http://www.biodiversitylibrary.org/) are have excellent examples of large-scale databases

utilizing literature. However, regional networks such as the Southeast Regional Network of

Expertise and Collections (http://www.sernec.org/) and Southwest Environmental

Information Network (http://swbiodiversity.org/seinet/collections/index.php) can play an

vital role in this process by identifying and mobilizing locally and regionally important

literature. Regional networks can be particularly effective at mobilizing more obscure forms

of literature that are only deposited in libraries within their region.

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Chapter 2: Spatial patterns of botanical exploration in North Carolina: a study using local

floras

Local floras provide important information for biodiversity studies (Palmer 2005, Funk 2006). Optimally, studies of plant distributions should utilize georeferenced locations based on properly identified herbarium specimens (Rich 2006). In reality, these data are available for few taxa and geographic areas. For this reason, local floras provide a good representation of the species present over broad areas (Palmer 1991). A local flora is an exhaustive floristic study completed for a specific geographic area. The flora is based on field-collected voucher specimens that are deposited in herbaria. These studies typically investigate multiple plant communities and tend to span more then one field season. Thus, such investigations provide a comprehensive picture of the floristic composition of the studied area. Local floras in North Carolina cover areas of varying size, from small islands and state parks to entire counties.

The spatial patterns of botanical knowledge have strong implications for conservation planning (Tobler et al. 2007). That is, it is difficult to protect species and their associated communities when basic information on distribution and abundance is lacking (Possingham et al. 2007). It has been recognized that many areas worldwide are still in need of baseline botanical information (Kier et al. 2005). For example, Kier et al. (2005) rated the southeastern United States as only moderate to good in terms of the quality of existing botanical data. Examination of the geographic patterns of botanical research within such regions can yield information about areas in need of floristic study.

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The few studies that have attempted to address the survey gaps in botanical exploration have utilized individual plant collection locality data, rather than complete floristic surveys. For example, one previous study identified survey gaps in Guyana by analyzing plant collection sites and environmental density (GIS-derived environmental variables) as a surrogate for species level diversity (Funk et al. 2005). Another study developed a GIS model that analyzed the collection localities of two well-collected genera (Soza et al. 2000), integrating location, time and activity of specific collectors to establish poorly documented areas of southern California. The only study to investigate the location of poorly collected areas in the southeastern Unites States was Duncan (1953). Similar to Soza et al. (2000), Duncan (1953) analyzed the collections of a few representative genera. All of these studies utilized surrogates of plant diversity information since complete collection information of all taxa is extremely difficult to obtain.

Integration of local floristic studies, as opposed to individual collection events, offers an opportunity to improve assessment of botanical patterns, and patterns of botanical exploration. Analysis of published floras may provide a less biased depiction of botanical knowledge since a concerted effort is made (by the flora authors) to collect all taxa of vascular plants over multiple seasons and habitats. Analysis of the published floras, therefore, may avoid the potential pitfalls associated with biases and preferences in plant collecting, as well as in choosing specific taxa for study (e.g., for range analysis). Furthermore, obtaining all local floras for a given area is a relatively easier task than obtaining every collection event that has ever taken place. For these reasons, local floras were chosen in this study to be used as an appropriate surrogate of botanical knowledge.

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Understanding the floristic uniqueness of specific geographic areas is important for conservation of biodiversity (Ertter 2000). This understanding is crucial if we intend to make informed decisions about acquisition and protection of lands, especially with limited resources that must be allocated efficiently (Stein 2002). These issues are of particular importance in North Carolina, which is ranked 11th for vascular plant diversity and ranked 13th for most plants at risk of extinction in the United States (Stein 2002). Additionally, the flora of North Carolina is far from fully cataloged. There have been 83 new taxa described from North and South Carolina since 1968 and at least 432 new aliens have been documented during this same period (Alan Weakley, unpublished).

Analyzing the patterns of botanical exploration can provide important insights into the development of efficient plans for future expeditions into botanically little known areas (Funk et al. 2005). A few past studies have shown a tendency for botanical knowledge to be related to cities and transportation routes (e.g., Tobler et al. 2007). Additionally, counties containing universities in the United States tend to be better explored botanically than those counties without such institutions (Moerman and Estabrook 2006, Pautasso and McKinney 2007). These non-random errors in the data introduce bias into larger scale analyses of botanical information. It is therefore important that these biases be addressed so that efforts can be focused on lesser-known areas.

This study addressed three main questions: (1) How are North Carolina floras spatially distributed? (2) Are there 'survey gaps' of floristic exploration in North Carolina? (3) Are floras located close to herbaria in North Carolina?

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Materials and Methods. DATA COLLECTION AND DATABASE DEVELOPMENT. A flora is a list of plants for a given area. The area must be unambiguous and the study location should be clearly stated. Detailed geographic location is critical to the evaluation of a flora. If a flora's geographic boundaries are not known, the species list has limited capacity to assess specific species distributions, range extensions and importance of occurrences. Furthermore, it can be difficult to add supplementary information for further floristic analysis (e.g., elevational range). For these reasons, only complete floras are included in this analysis. For example, if a list is restricted taxonomically (e.g., *Poaceae* excluded), or seasonally (e.g., 'spring floras') they are excluded from the present analysis.

The floras were obtained from standard literature searches (e.g., Agricola), bibliographies of other known floras and manual journal scanning (e.g., *Castanea, Journal of the Elisha Mitchell Scientific Society*) and personal communications. In addition, I searched the library catalogs of all North Carolina colleges and universities in order to locate unpublished theses and dissertations. This method was found to be more reliable than searching the Dissertation Abstracts database. Floras were obtained in hard copy via electronic download or through Interlibrary Loan. Each publication was then reviewed to make sure it fit the criteria listed above.

It was not possible to digitize the exact boundary of each study area, since study area maps were not provided for all studies, making it difficult to draw precise polygons. For this reason, the minimum and maximum latitude and longitude were recorded for each flora. When a map was not provided these values were estimated based on the study area description from the study methods. The floras were geo-referenced using Google Earth (earth.google.com). Google Earth uses geographic coordinates (latitude/longitude) on the

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World Geodetic System of 1984 (WGS84) datum. The complete dataset consisted of 98 flora sites from 89 publications (Appendix B). Analyses were carried out in R software version 2.9.2 (R Development Core Team 2009) with the **spatstat** and **sp** spatial analysis packages (Baddeley and Turner 2005, Pebesma and Bivand 2005).

POINT SIMULATION AND DISTANCE MAP. Since the exact boundaries of each flora were not always known, a point simulation model was used to represent the location of each flora in geographic space. This process consisted of two steps. (1) Unique polygons were generated from the minimum and maximum latitude and longitude points for each flora. (2) 50 random points were sampled within each of the 98 polygons. The result was 4900 unique points that fell inside all of the polygons.

A distance-based raster was generated in order to visualize where survey gaps exist in North Carolina. The model was based on the assumption that a flora's usefulness will diminish at a distance of 20 linear kilometers. Five classes were used to show distance gradations of up to 100 kilometers. This method may be overly conservative by assuming all floras have the same decay in usefulness with distance. In reality, a larger size study could be more useful at a greater distance than a small study. However, the overall goal of this study is to visualize where floras have been conducted and target areas for future exploration. Therefore, the present model seems appropriate given the geographic extent of this study.

SITE SELECTION SIMULATION. A site selection simulation was conducted to assess if the flora sites were significantly clustered around North Carolina herbaria. The process consisted of dividing North Carolina into hypothetical study sites (grid cells) and generating an expected distance between the hypothetical sites and North Carolina herbaria under random conditions using a bootstrap procedure (Efron 1979). This was done by dividing North Carolina into 6481 hypothetical sites (~2000 hectares each, a typical flora size) and measuring the distance of each site to the nearest herbaria where floras have been conducted (BOON, DUKE, WNC, WCUH, NCSC, NCU; acronyms follow Thiers 2009). Ninety-eight hypothetical sites were sampled 10,000 times to generate a sampling distribution using a bootstrap procedure. This random distance simulation was then compared to the actual distance of floras to the closest herbarium. Two herbaria were dropped from this analysis since only one flora was conducted at each (UNCC and University of North Carolina, Pembroke); their inclusion would have overly biased the actual distance measures. All other herbaria were the home institution for multiple studies.

Results. SURVEY GAPS. In general, floras are distributed throughout the state of North Carolina, from the coast to the mountains (Fig. 1). The outer Coastal Plain has been well documented floristically. In addition, 11 floras have been conducted on all or part of the Outer Banks islands, though it is difficult to visualize due to the narrow shape of the Outer Banks islands (see in Appendix B Kearney 1900, Burk 1961, Au 1974, Resource Management and Visitor Protection Staff 1977, Dickerson 1978, Mayes 1984, Bland 1990, Williams 1991, Stalter and Lamont 1997, Stalter and Lamont 1999, Kelly 2006). However, the distance based raster map shows some obvious geographic gaps in botanical exploration.

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The inner Coastal Plain has some large areas with little intensive botanical exploration. In addition, the Piedmont has several areas that lack floras. For example, the northern portion of the Piedmont currently only contains one small flora. The central and southern Blue Ridge Mountains (e.g., Madison and Cherokee Counties) also have significant gaps.
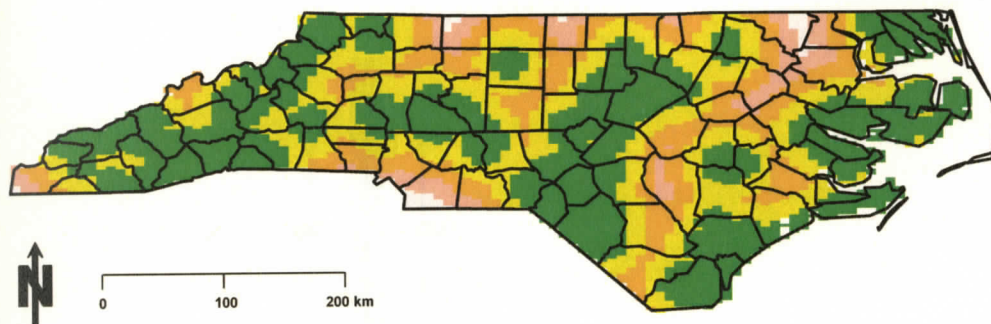
Fig. 1. North Carolina county map showing linear geographic distance from flora points. Distance classes are in 20 kilometer intervals. Green areas are 0 - 20 kilometers from a given flora point.

SITE SELECTION SIMULATION. The site selection simulation found that the floras tend to be located closer to herbaria then would be expected by chance (Fig. 2). The bootstrap procedure yielded an expected average distance of 97.18 kilometers (95% confidence intervals = 85.67 and 109.05). The 98 flora sites were significantly clustered around herbaria. Wilcox test with $\mu = 97.18$, p-value = < 0.001, 95% confidence interval = 46.39609 and 65.76086.
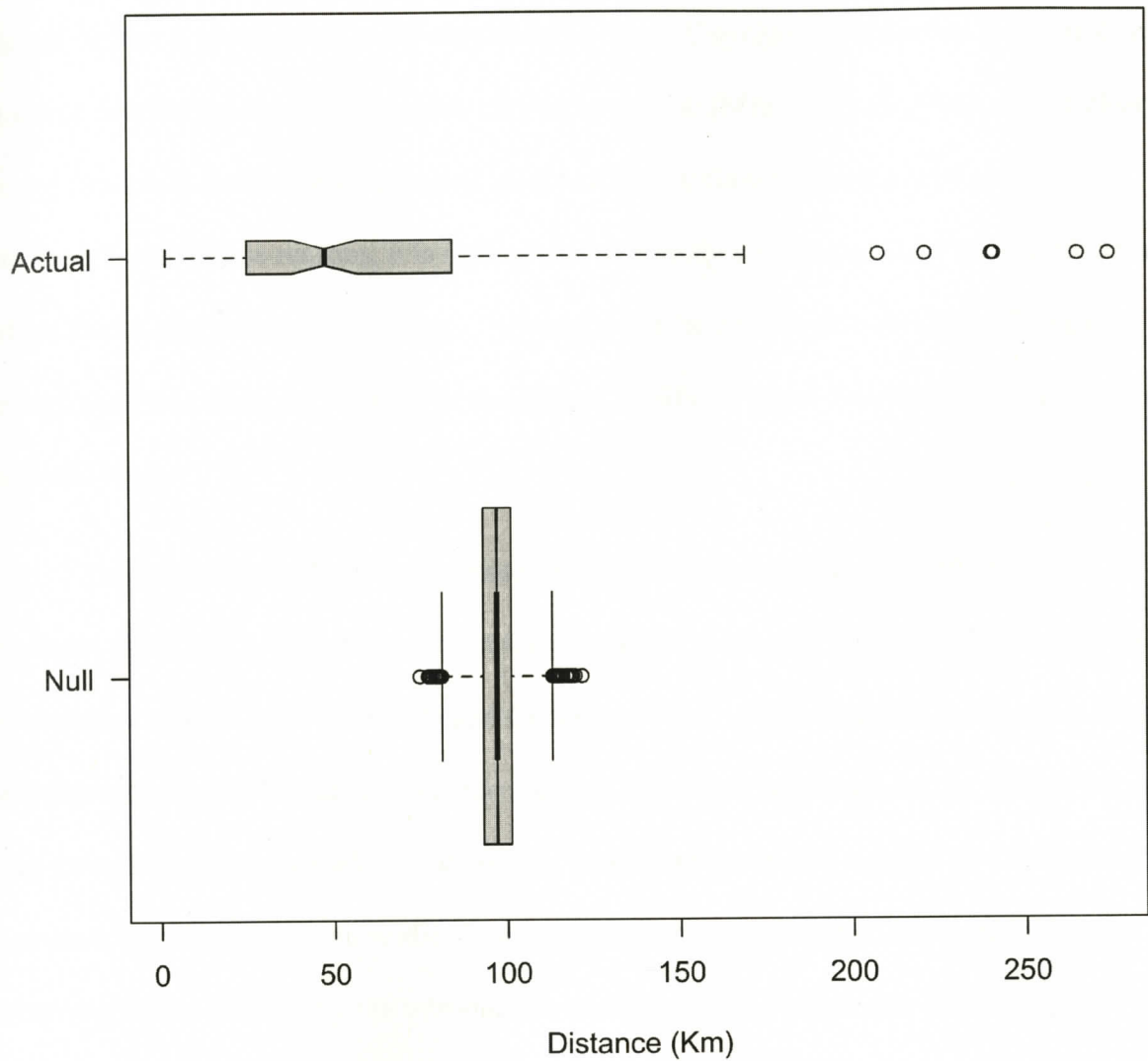
Fig. 2. Boxplot showing the actual distance from floras to herbaria and the simulated null expectation. Boxes are drawn with widths proportional to the number of observations in the groups.

Discussion. This study indicates that significant areas of North Carolina lack good

floristic information. These results are grim in light of the fact that overall declines in plant

collecting in the United States have been documented (Prather et al. 2004). Many of the

floras used in this study were conducted as part of Master's thesis projects. This type of project often gives plant systematists and plant ecologists a foundation in plant diversity and identification. A preliminary study conducted in North Carolina indicates that the number of students conducting floristics research may be in decline (Mitchell et al. 2008). It is unclear how a decline in trained plant scientists might affect our future knowledge of plant biodiversity. For these reasons, it is critical that new study sites be carefully selected in areas where floristic information is lacking. This model can be used to plan for future floristic research and site selection. That is, botanists will be able to target their research in under-explored areas.

This model may also help to locate existing plant lists for areas of interest. For example, floras can act as a snap shot of the plants of a given area allowing for the analysis of change over time (e.g., Harrelson and Cantino 2006). In North Carolina publication dates of floras range from the year 1860 to the present. This time line allows for the assessment of long-term floristic change. Floras can also be used to understand the spread of exotic species over time. Specifically, some studies have utilized floras to understand how native communities are affected by the introduction of exotic species (Qian and Ricklefs 2006). Floras conducted at high elevations can be utilized to document elevation range shifts of species with changing climatic conditions. While it is clear that range shifts are taking place globally, much remains to be learned about how individual species will respond to recent changing climatic conditions (Walther et al. 2002).

The point simulation model and distance map proved to be an effective strategy for assessing spatial patterns of botanical exploration. Nevertheless, the model has two possible limitations. First, it is possible that there are floras that have not yet been found. Many of the

floras used in this study were somewhat obscure and difficult to obtain. For this reason, it seems feasible that some studies were overlooked during the course of this study. Second, this model focused on the state of North Carolina only. It is possible that some floras from Virginia, Tennessee and South Carolina may be very close to the North Carolina border. Ideally, models of botanical exploration will be conducted at the regional or continental scale to reduce the bias that political boundaries can introduce. It is therefore essential that the legacy information be mobilized so that the botanical community can advance the understanding of biodiversity at local, regional and continental scales.

Site selection bias was detected using the simulation model. Similar to previous studies that have examined the 'botanist effect,' this study found that floras are clustered around research institutions and populated areas (Moerman and Estabrook 2006, Pautasso and McKinney 2007). Most of the herbaria in North Carolina are located in large cities. The model used in this study assumes that the closest herbarium to a study was the home institution of the author. Indeed this was the case for a large majority of the floras. However, the clustering around herbaria could also be a result of the availability of infrastructure and supplies of these large cities. Whatever the cause, this spatial bias in site selection partially explains why some areas in North Carolina have not yet been thoroughly explored botanically.

In a time when so many species are threatened by anthropogenic causes such as land use and climate change, it is essential that the botanical community continue to document the flora of North Carolina. This study provides a way for future investigators to locate the areas most in need of floristic study.

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Chapter 3: Patterns of native and exotic plant richness along an elevational gradient from sea level to the summit of the Appalachian Mountains, U.S.A.

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 humped-shaped pattern is the most typical pattern, with a monotonic pattern also frequently encountered (Rahbek 2005). However, when complete gradients are sampled a humped-shaped pattern is expected for plants and vertebrate taxa. In order to detect humped 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 Stohlgren et al. (2005) made use 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

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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, I examine whether native and exotic species show similar richness patterns along the elevational gradient. I 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 from North Carolina, USA (Appendix C). These 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 km^2 to 81 km^2. 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, M.W. Denslow, unpublished). Even still, 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, I determined total 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 danger

that the richness counts can be affected by the different taxonomic concepts used in the

original sources. The effect of different taxonomic concepts was assessed for five floras from

this dataset. The taxonomy was reconciled for five floras in order to assess the effect on

richness counts. This analysis indicated that studies at the level of species would not be

severely effect by using data from different sources with different taxonomic concepts

(Appendix D). The difference in richness counts ranged from 0.3% to 2%, with an average

difference of < 1%.

I used sixty-eight floras located along a large elevational gradient (0 - 2037 m). This

gradient ranges from the Atlantic Ocean, 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, I constructed a linear

regression model that included area, year and elevation. I $\log_{10}$ transformed area, exotic,

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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 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 I 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 preselect the number of knots (join points of piecewise function). I followed the method of Durrelman and Simon (1989) and Harrell (2001, 2009) by placing knots at fixed quantiles of the predictor's distribution. The number of knots were selected 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. I 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

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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.

I 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, I only present results from models without interaction terms. To determine if spatial regression models (i.e., spatial autoregressive) would be appropriate, I 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 (Appendix E). 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

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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.

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
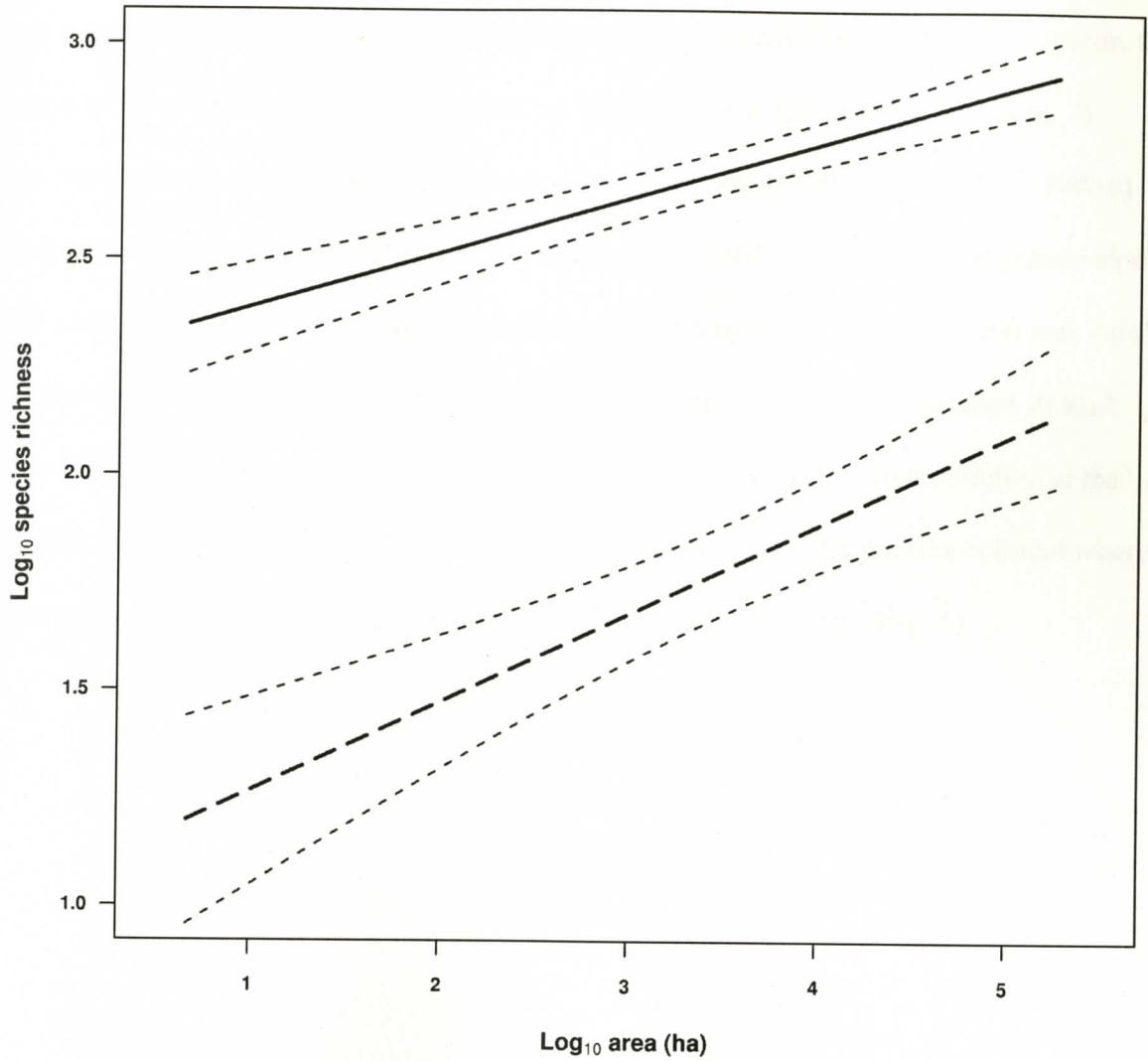
Fig. 1 Species area relationship for native species (solid line) and exotic species (long dashed line), short dashed lines are 95% confidence intervals for the mean. The prediction lines are based the full regression model including area, year and elevation. The lines indicate log_{10} species richness 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.

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 species richness (Table 1). Elevation was not a significant variable in the exotic species richness model (Table 1). In other words, the slope of the exotic species response was not significantly different from zero (Fig. 3). However, exotic richness was consistently low at the highest elevations (above 1500 m). Total species richness (native plus exotic richness) showed a humped 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).
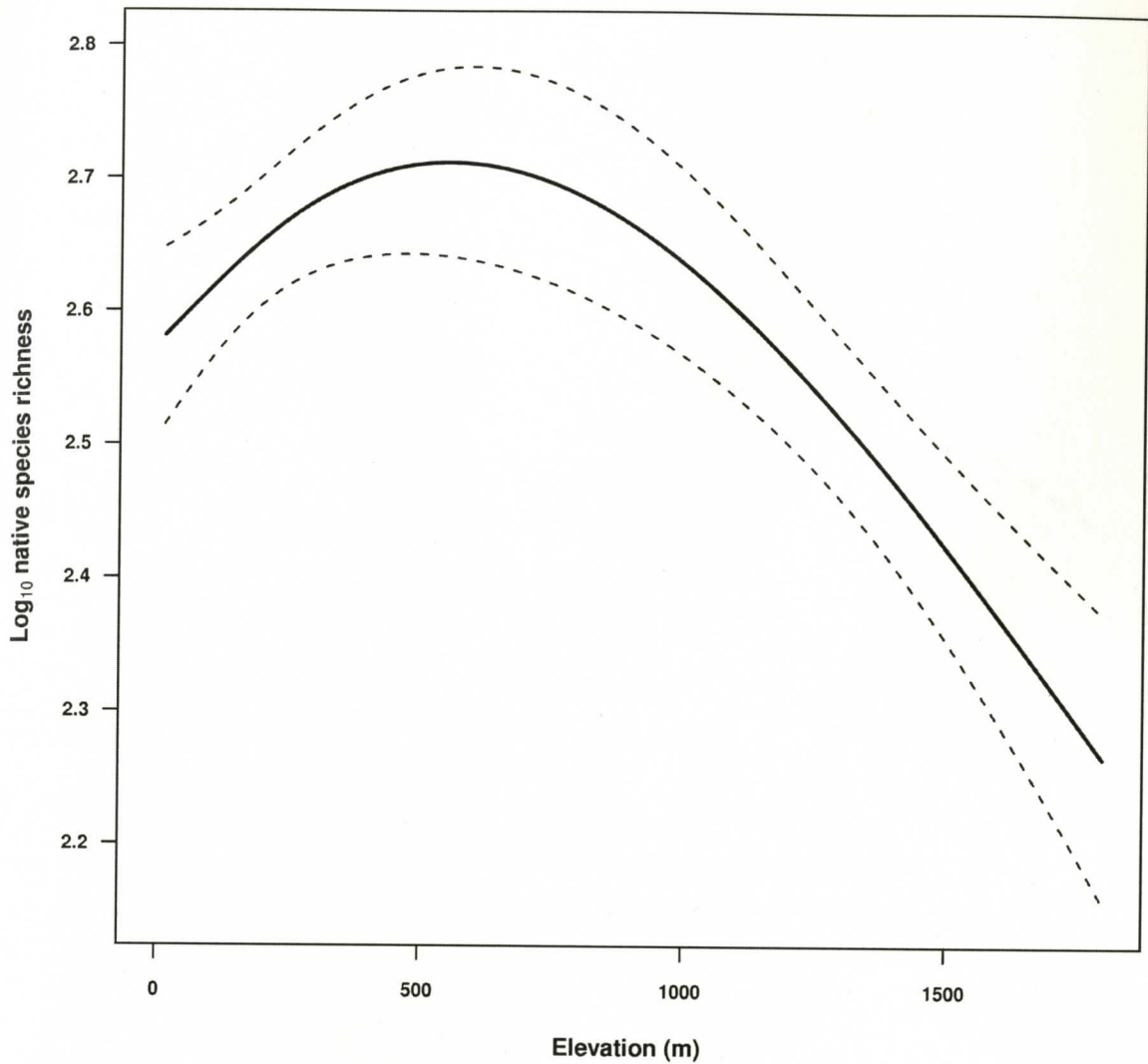
Fig. 2. Species elevation relationship for native species, short dashed lines are 95% confidence intervals for the mean. The prediction lines are based the full regression model including area, year and elevation. The lines indicate $\log_{10}$ species richness for $\log_{10}$ area of 3.217 and the year 1974. See Table 1 for complete regression results.

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.
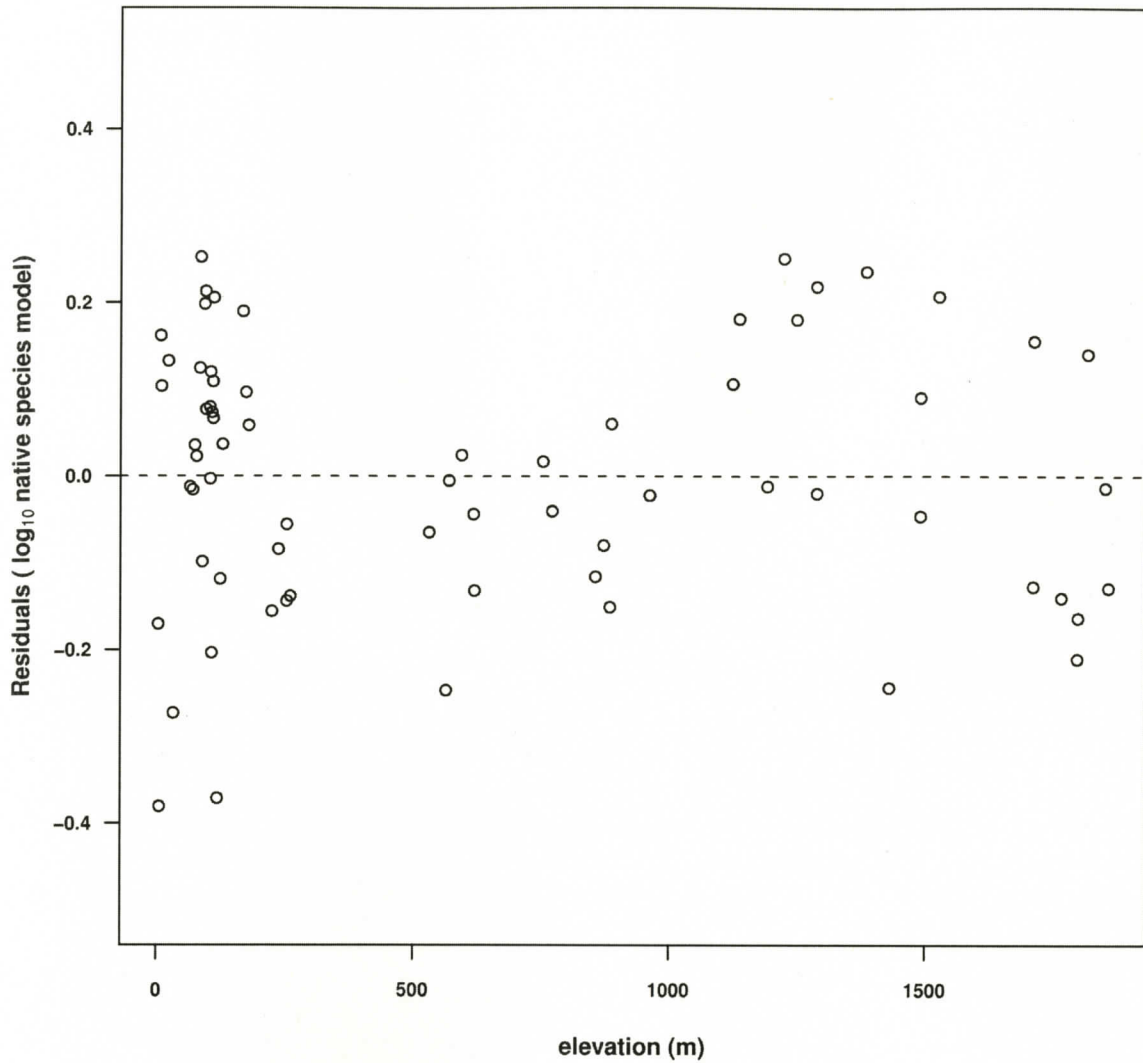
Fig. 4. Residuals from native species model, including area, year and elevation as independent variables, plotted against elevation.
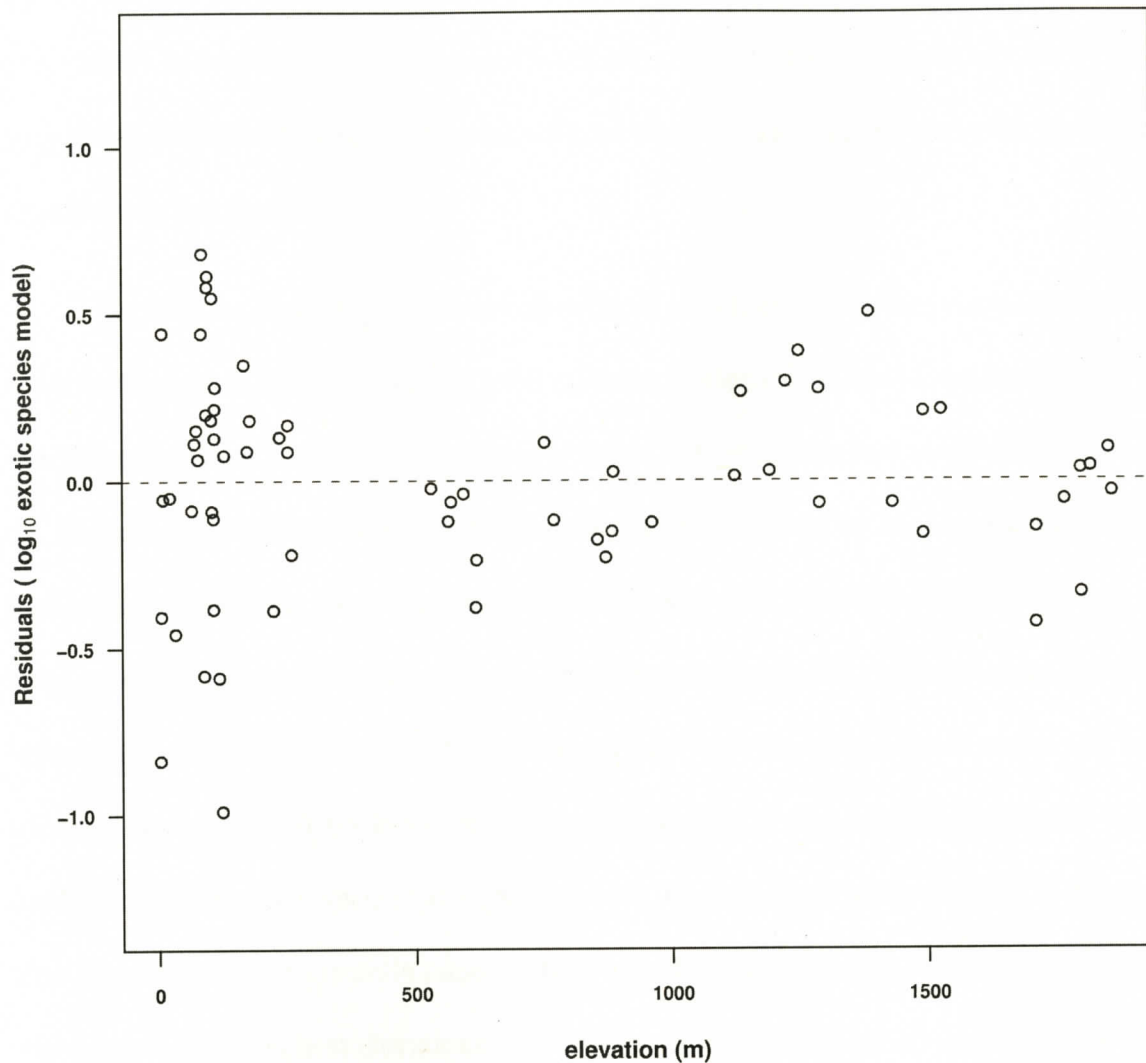
Fig. 5. Residuals from exotic species model, including area, year and elevation as independent variables, plotted against elevation.

Discussion. In this study, native and total species 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 showed no statistically detectable trend along the elevation gradient. The few previous studies that have examined exotic richness patterns

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along elevational gradients have found either a linear decline (Becker et al. 2005, Mallen-Cooper and Pickering, 2008), or a humped shaped pattern (Tassin and Rivière 2003, Arévalo et al. 2005). In contrast, I found no significant effect of elevation on exotic richness, suggesting that other 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). This indicates 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

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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 increased by 290 taxa in the past 40 years, while 432 exotic taxa have been discovered during the same period (A.S. Weakley, unpublished). Therefore, it may be difficult to distinguish between sampling effects and the detection of novel species introductions.

The differing patterns of native and exotic species richness documented here are perhaps not surprising, considering that native and exotic species have been shown to differ in richness patterns along other environmental gradients in some areas (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 fact that native and exotic species richness patterns differ along environmental gradients suggests that the mechanisms governing richness may differ for the two groups. 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* Takhtakjan 1986) may have distinct assemblages of exotic taxa (e.g., those present in the Coastal Plain vs. the Blue Ridge), these assemblages 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,

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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 and could lead to the

observation of different patterns.

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, unpublished 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 (Fig. 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. For this reason, it seems possible the hump shaped

pattern displayed for native species (Fig. 2) may have been even more pronounced in the

absence of humans. In addition, human impacts may obscure richness patterns by altering

native diversity through land use changes, and by introducing exotic species. The majority of

exotic plant species in the United States were deliberately introduced for horticultural or

agricultural reasons (Mack and Erneberg 2002). As such, exotic richness is often strongly

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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).

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 patterns may in fact be idiosyncratic due to factors such as disturbance history. More insight could be gained by comparing native and exotic richness patterns along these gradients. For example, this study contrasts with the results of Palmer (2006) 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. I found the opposite, with native richness being more strongly related to physical gradients and better predicted by the regression models. There is an abundance of literature related to total species richness of various organisms along elevational gradients (Rahbek 2005). However, more studies are needed to examine the patterns of native and exotic species in mountain areas. Additional studies will inform our knowledge of both native and exotic species to gain a better understanding of diversity patterns.

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APPENDIX B. Author and year for citations used in this analysis. Complete reference information can be found in Appendix A.

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Bradshaw 1987

Britt 1960

Bruton 1968

Burk 1959

Burk 1961

Corda 1982

Curtis 1834

Dickerson 1978

DuMond 1970

Elam et al. 2009

Feil 1987

Floyd 1996

Gupton 1960

Hoffman 1964

Horton 1957

Houck 1956

Johnson et al. 1991

Jones 1971

Jones 1973

Kearney 1900

Kearney 1901

Kelly 2006

Kessler 1956

Kologiski 1977

Krings and Franklin 2004

Lacey 1977

Larke 1991

LeGrand and Sorrie 1997

Levy 1976

Livengood 1972

Mayes 1984

McCormick and White 1993

McLeod 1988

McNeely 1960

Memminger 1915

Michael 1969

Morgan 1962

Morris 2007

Musselman et al. 1977

Palmer 1990

Peattie 1928

Pittillo and Lee 1984

Poindexter 2006

Pultorak 1969

Ramseur 1960

Resource Management and Visitor
Protection Staff 1977

Rodgers and Shake 1968

Rodgers and Shiflet 1978

Rodgers 1969

Rohrer 1983

Russo et al. 1993

Sawyer 1968

Shelingoski et al. 2005

Sieren and Warr 1992

Sieren 1982

Sieren 1984

Sieren 1992

Skean 1982

Smith 1977

Smith and Patti 1995

Sorrie et al. 2006

Stalter and Lamont 1997

Stalter and Lamont 1999

Stratton and White 1982

Strickland 2000

Swab 1990

Taggart 1973

Taylor and Cooper 1987

Taylor 1974

Tucker 1972

Ware 1973

Warren et al. 2004

Wells 1970

White and Pyne 2003

White 1982

White 2003

White et al. 2002

Wichmann et al. 2000

Williams 1991

Wood and McCarthy 1886

APPENDIX C.

Appendix C. Author and year of the floras used in the elevation richness analysis. See Appendix A for complete citation information.

Beard 1958	Jones 1971
Blair 1967	Jones 1973
Bradshaw 1987	Kearney 1901
Bruton 1968	Kennemore 1995
Burk 1959	Kessler 1956
Corda 1982	Krings and Franklin 2004
DuMond 1970	Lacey 1977
Feil 1987	Larke 1991
Floyd 1996	McCormick and White 1993
Gupton 1960	McLeod 1988
Hoffman 1964	McNeely 1960
Horton 1957	Memminger 1915
Houck 1956	Michael 1969
Johnson et al. 1991	Morgan 1962

Musselman et al. 1977

Palmer 1990

Pittillo and Lee 1984

Poindexter 2006

Pultorak 1969

Ramseur 1960

Rodgers and Shake 1968

Rodgers and Shiflet 1978

Rodgers 1969

Rohrer 1983

Russo et al. 1993

Sawyer 1968

Skean 1982

Smith 1977

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Stratton and White 1982

Swab 1990

Taggart 1973

Taylor 1974

Tucker 1972

Ware 1973

Wells 1970

White and Pyne 2003

White 1982

White 2003

White et al. 1992

Wichmann et al. 2000

APPENDIX D. Table of taxonomic concept comparisons

Table D1. Richness counts at the level of species for
two different taxonomic concepts

Flora Citation	Species[a]	Species[b]	% diff.
Tucker 1972	677	693	**2**
Pittillo and Lee 1984	596	590	**1**
Bradshaw 1987	430	426	**0.9**
Michael 1969	328	327	**0.3**
Rohrer 1983	355	353	**0.5**
average			**0.94**

[a] Concept of Radford et al. 1968, [b] Concept of Weakley 2008

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APPENDIX E. Results of Moran's I test

Table E1. 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

BIOGRAPHICAL SKETCH

Michael Ward Denslow Jr. was born in New Rochelle, New York, on the 19th of July 1977. He attended elementary and middle school at Rye Country Day School in Rye, New York. He graduated from the Kent School in Kent, Connecticut in 1995, where he was awarded the Ogden Nature Prize for his interest in Natural History and Ecology. In 2000, he graduated from the University of Denver in Denver, Colorado with a Bachelor of Arts degree in Geography and a minor in Biology. Michael was awarded a Graduate Certificate in Geographical Information Science from the Department of Geography and Planning at Appalachian State University in Boone, North Carolina in May 2009. He completed his Master of Science degree from the Department of Biology in December 2009.