PATTERN AND PROCESS IN RARE PLANT CONSERVATION:

AN ASSESSMENT OF THE SOUTHEASTERN U.S.

Sarah E. Marcinko

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Approved by:

Peter S. White
John L. Randall
Dean L. Urban

ABSTRACT

Sarah E. Marcinko: Pattern and Process in Rare Plant Conservation: An Assessment of the Southeastern United States
(Under the direction of Peter S. White)

The development of conservation policy for rare plant species is informed by large-scale patterns of distribution and abundance as well as the processes that generate them. I collected data on 224 rare vascular plants in the Southeastern U.S. to characterize patterns of rarity at ecoregional scales, among broad habitat types, and with respect to taxonomic group size. Rare species diversity is highest in Appalachian/Blue Ridge Forests and Southeastern Conifer Forests ecoregions. Most rare plants are concentrated in woodland and glade habitats and larger taxonomic groups.

A case-study experimental approach was adopted to explore the significance of reproductive biology in the persistence of a globally imperiled Southeastern endemic plant, *Ptilimnium nodosum*. The species has a phenologically regulated mixed mating system dependent on insect-mediated pollination. Moderate reproductive output and high seed germinability suggest environmental conditions, not mating system, play a critical role in regulating the species' distribution and abundance, and favor high immediate fitness gained by vegetative reproduction.

To my dad who gave me perspective

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Conservation biology is a discipline with a deadline (Ricketts et al., 1999a). Human-induced environmental changes are occurring at a rapidly increasing pace and have severely impacted species diversity and composition. The accelerating and widespread loss of species is unprecedented (Thomas et al., 2004) and the task of conserving biodiversity is considered to be one of the most important global environmental challenges today. The scale of loss is daunting and most conservationists have recognized the need for prioritizing areas for conservation to make recovery and protection efforts more efficient and effective, often before all relevant data is collected.

Conservation strategies have largely focused on patterns of diversity, specifically how to maximize the number of species that can be protected within a particular geographic region. Species inventory data are fundamental to the development of conservation plans or "portfolios," which represent the full array and diversity of native species, communities and ecosystems within an area (TNC, 2004). The criteria for identifying areas of highest conservation value is wide-ranging and includes high species richness (Ricketts et al., 1999a), endemism (Meyers et al., 2000; Hobohm, 2003), rarity (Prendergast et al., 1993), endangerment (Dobson et al., 1997), unique phylogenies (Mace et al., 2003) and evolutionary histories (Sechrest et al., 2002), and degree of threat (Wilcove et al., 1998; Abbitt et al., 2000). Rare, threatened, or endangered species in particular are frequently the conservation targets captured by portfolios. Nonetheless, the reliance on threatened species lists or the identification of biodiversity patterns for the delineation of conservation areas often fail to address the ecological and evolutionary mechanisms that produced the patterns in the first place (Smith et al., 1993). The “flux of nature” (Pickett et al., 1992) ensures that the presence of a species at risk in a protected area does not guarantee its conservation. Dynamic natural processes in ecological communities and human-caused environmental impacts can lead to species turnover and loss even in areas set aside for conservation. Ensuring the viability of target species will often require more active management. Conservation of rare species must be guided by the biological attributes of the taxon, yet the lack of basic biological data has been implicated in the failure of many recovery plans, especially for plants (Pavlik, 1994; Schemske et al., 1994; Schultz and Gerber, 2002). What constitutes the most critical biological information has been the subject of much debate (Schemske et al., 1994). Most scientists will agree on the importance of incorporating ecological, genetic, and evolutionary processes in conservation and studies of autecology, demography, and reproductive biology abound.

In this thesis, I seek to combine conservation strategies of pattern and process. Specifically, I aim to identify patterns in rare plant species and natural areas of high conservation value as well as take a closer look at the fundamental processes responsible for maintaining diversity patterns. My focus is the Southeastern United States, an ecologically complex region rich in biological diversity. It is also a region that has undergone substantial environmental change, resulting in the loss of globally distinct habitats and communities (Ricketts et al., 1999b).

In the second chapter, I explore several patterns of rarity in the Southeast flora with respect to geography, ecology, and taxonomy. Here, rarity is a surrogate for extinction risk and is delimited by global conservation status ranks. To streamline and facilitate conservation efforts I use Natural Heritage program data to compile detailed information on 224 rare species. Specifically, I ask three questions: 1) How are rare plants distributed at the state and ecoregional scales? 2) Are rare plants clustered within particular habitat types? And, 3) How is rarity distributed among taxonomic groups? I show that rarity among plants is not randomly distributed across the Southeast and discuss some of the ecoregions, habitat types, and plant families that contain unusually high number of rare species.

In chapter 3, I take a case-study approach to address reasons for rarity and persistence in a federally endangered plant, *Ptilimnium nodosum* by examining the species' reproductive biology. Studies of reproductive biology are critical to the effective conservation and management of rare and endangered species (Hamrick et al., 1991; Karron, 1991; DeMauro, 1993; Weller, 1994). Demographic trends (survival, growth, and reproduction) directly influence population dynamics and biological/conservation status. Furthermore, differences in mating patterns can influence the amount and genetic structure within a species, which are believed to affect the evolutionary potential of a species and ability to adapt to a changing environment.

In addition to determining the mating system of *P. no*dosum, I examine the role of floral phenology and differential sex expression in regulating opportunities for mating. I show that the limited distribution and abundance observed in *P. nodosum* may not be a total consequence of its reproductive biology. The species is restricted to a unique and uncommon habitat type that is threatened by changes in dynamic processes, suggesting that environmental conditions, not mating system, may play a central role in population dynamics.

Finally, in the fourth chapter I combine the results from each chapter to discuss the application of this research to the conservation of Southeastern rare plants at landscape and local scales. I demonstrate how the identification of patterns of rarity in this region complement and improve upon other research contributions concerning plant conservation in the Southeast. I also discuss current management plans and ongoing research objectives for *Ptilimnium nodosum*. I conclude with some of the conservation challenges that complicate *P. nodosum* recovery efforts and make recommendations for future research.

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II. PATTERNS IN RARITY AMONG VASCULAR PLANT SPECIES IN THE SOUTHEASTERN UNITED STATES

Abstract

The objective of this research is to examine geographic, ecological, and taxonomic patterns in rarity among plants in the Southeastern United States in an attempt to inform and facilitate on-going conservation efforts. I collected data on 224 rare vascular plant species carrying a global conservation rank of G1-G2G3 to assess the distribution of rare plants at state and ecoregional scales. I show that Southeastern Conifer Forests and Appalachian/Blue Ridge Forests are especially rich in rare species. A closer examination of species-area relationships reveals several counties with unexpectedly high numbers of rare plants. I also explore the representation of rare plants in broad habitat types across the Southeast. Using a habitat classification scheme unique to the Carolinas, I then determine if species are over-represented in particular habitat types. Across the Southeast, rare plants are overwhelming distributed in woodland and glade habitats, particularly calcareous glades, woodlands, and prairies. In the Carolinas, rare plants were over-represented in Coastal Plain blackwater bottomlands and wet savannas and flatwoods. Finally, I examine the distribution of species within families and show that most Southeastern plant families only have three rare plants or less and small plant families consistently contain fewer rare species. Several families were surprisingly over-represented in rare plants, particularly the Isoetaceae and Brassicaceae.

Together, these patterns suggest a high degree of predictability in the distribution of rare plants within the Southeast.

Introduction

There are over 4500 native vascular plant species in the Southeastern United States (Stein et al., 2001). Within the USA, the Southeast ranks among the top “hotspots” in terms of native plant (Ricketts et al., 1999a; Qian, 1999; Stein et al., 2001) and ecosystem diversity (Noss et al., 1995; White et al., 1998). While considerable effort has been made in describing regional biodiversity patterns with respect to broad and small scale environmental variation, a glacier-free evolutionary history, and historical disturbance regimes (Delcourt and Delcourt, 1998; White et al., 1998; White and Miller, 1998), these mechanisms also provide a valuable opportunity to examine patterns in regional rarity and can potentially inform the on-going process of plant conservation in the Southeast.

Regional studies of rarity in the Southeastern U.S. have predominantly explored patterns of plant endemism. Estill and Cruzan (2001) compiled county-level distribution data on 482 endemic species to identify regional centers of endemism. They found that endemic species also tend to be regionally rare and demonstrated geographic clumping of endemics. Similarly, Loehle (2006) expands on the work of Estill and Cruzan (2001) to describe hotspots of endemism with regard to habitat types. He comments on the concentration of endemics in, among others, pine flatwoods, sandhills, and savannahs in the mid-Atlantic Coastal Plain as well as the cedar glades in the Central Basin of Tennessee and granite outcrops throughout the Piedmont Plateau. Others have assessed rarity and endangerment in particular communities (Grossman, 1994; Patterson et al., 1994; Noss et al., 1995) and habitats, including coastal plain wetlands (Sutter and Kral, 1994; Edwards and Weakley, 2001; Sharitz, 2003), hardwood forests (Imm et al., 2001), peat bogs (Stewart and Nilsen, 1993), glades and prairies (Platt, 1951; Baskin et al., 1995; Allison and Stevens, 2001; Baskin and Baskin, 2003; Lawless et al., 2006), and longleaf pine forests (Walker, 1993; Gray et al., 2003).

Most rare plants in the Southeast are naturally rare (Rabinowitz, 1981; Owen, 2002), although many factors influence the rarity of species (Fiedler, 1986; Fiedler and Ahouse, 1992), including their ecology, population biology, and taxonomy. More recently, considerable effort has been spent investigating whether rare species are randomly distributed among taxa in an attempt to better understand processes that lead to rarity (Domínguez Lozano and Schwartz, 2005) and forecast which species are most vulnerable to extinction (Schwartz, 1993; Edwards, 1998; Edwards and Westoby, 2000). If rarity is clustered in particular groups, it suggests that predisposition to rarity may be governed by intrinsic characteristics (e.g. taxon size) and attention should be directed to those species within groups with high rates of rarity that are not presently threatened (Lockwood et al., 2002; Pilgrim et al., 2004).

Identifying patterns of rarity and vulnerability, particularly at scales relevant to conservation planning, is becoming increasingly important in light of current rates of biodiversity losses (Abbitt et al., 2000; Pearman et al., 2000). The Southeast heads the list of the highest number of endangered ecosystems of any region in the country (Noss et al. 1995; Stein et al., 2001; Owen, 2002). Rapid population growth, development, and loss of biologically rich communities in the Southeast have significantly affected the distribution and abundance of many plant taxa and pose a serious threat to species already limited in population size, occurrence, and geographic extent (Wilcove et al., 1998). Here, in an attempt to streamline and facilitate conservation efforts, I use a database of rare species in the U.S. to describe several patterns of rarity in the Southeast flora by addressing the following questions:

(1) How are rare plants distributed at state and ecoregional scales?

(2) Are rare plants clustered within particular habitat types?

(3) How is rarity distributed among taxonomic groups?

Methods

Data Collection

The geographic extent for the Southeast used in this study follows the coverage area reported in Weakley (2006) and includes the Carolinas, Virginia and D.C., West Virginia, Maryland, Delaware, Kentucky, Tennessee, Alabama, Mississippi, the Florida Panhandle and Northeastern Florida (Fig. 2.1).

A database of Southeastern rare vascular plant species was compiled using Natural Heritage Program data available through NatureServe (www.natureserve.org). Initially developed by the Nature Conservancy, NatureServe assesses species vulnerability on several criteria, including occurrence and extent of occurrence, population size, geographic range, trends in population status (short- and long-term), listed threats, intrinsic vulnerability, and the number of protected populations (Master et al., 2001; Andelman et al., 2004). The Natural Heritage ranking system is a reliable protocol for identifying vulnerable species (Master et al., 2001; Andelman et al., 2004; Keith et al., 2004) and NatureServe is considered to be the most comprehensive database in the United States for at-risk species (Regan et al., 2004; Mills and Schwartz, 2005). Although NatureServe ranks have no official role in the federal listing of species in the United States, they do provide a more accurate assessment of species endangerment (Master et al., 2001) and inform management decisions for private and public organizations, government agencies, academia, and the general public (Regan et al., 2004).

There are many ways to describe rarity (Kunin and Gaston, 1993) and many factors operating at a range of spatial scales may determine the abundance or rarity of species (Schemske et al., 1994). For the purpose of this analysis and within the NatureServe database, rarity is a surrogate for extinction risk and is delimited by conservation status ranks available at the global, national, and subnational scale; here, rare species were assessed at the global level (G). All species carry a rank on a one-to-five scale, ranging from critically imperiled (G1) to common, secure species (G5). Conservation ranks are primarily based on the number of occurrences of a species and the degree to which threats are perceived. However, distinguishing species that are intrinsically rare from those that have become rare due to human activities is not possible (Stein et al., 2001) as most rare species are predisposed to threat on account of habitat specialization, small population size, or narrow geographic distribution (Rabinowitz, 1981; Kruckeberg and Rabinowitz, 1985). The scope of this analysis includes G1 and G2 (imperiled) species, which are found in <5 and 6-20 populations worldwide, respectively. Species with ranks listed as G2G3 were also included (<100 populations). Historically occurring species (GH) and those presumed extinct (GX), however, are omitted since the intent of this paper is to provide current trends and information on rare plants.

Taxonomic classification of the NatureServe database follows Kartesz (1999) although botanical nomenclature follows Weakley (2006) for the area of analysis. Rare infraspecies are included in analyses, but questionable taxa not recognized by Weakley were omitted. Similarly, recent taxonomic revisions that have resulted in changes in global conservation status ranks higher than G2G3 were also excluded. Consequently, a total of 224 Southeastern rare plants were the basis for all subsequent analyses. For each species, I collected information regarding taxonomy, geographic range, conservation status, and ecological attributes.

How are rare species distributed in the Southeast?

To examine species distribution patterns and endemism across the Southeast, I first examined the aggregation of rare plants at the state scale. While many political and social decisions regarding rare plant management occur at this level, states are, of course, artificial constructs on larger, ecological landscapes (Master et al., 2001). More recently, the conservation community has been leading conservation efforts beyond state boundaries in order to capture both vulnerable species and ecological communities (TNC, 1996). An ecoregion based approach targets geographically distinct assemblages of natural communities that, to a large degree, share species, dynamics, and environmental conditions (Ricketts et al., 2001). Accordingly, using data compiled by Ricketts and others (1999b), in addition to county and ecoregional spatial data, I used a GIS to classify the 224 rare plants of this analysis into eight terrestrial ecoregions (Fig. 2.1; Table 2.1). To examine the effect of area on rare species diversity patterns at a finer resolution, I used species distribution data at the county level from Weakley (2006), USDA PLANTS (2006), and NatureServe databases (2006), and calculated the number of rare species per county. Linear regressions of the number of rare species vs. county area were then performed for each ecoregion. Those counties located in ecoregions not well-represented in the area of analysis (Mississippi Lowland Forests and Northeastern Coastal Forests) were combined into ecoregions most similar in composition.

Are rare plants clustered within particular habitat types?

Ecological information was used to assign rare plants to one of the 29 habitats defined by Weakley (2005) for the 3301 native plant species of the Carolinas. This classification scheme is based on vegetation classification data from Schafale and Weakley (1990), NatureServe (2003; 2005), Faber-Langendoen and Tart (2001), and the Carolina Vegetation Survey (2005). Each habitat consists of distinct species assemblages. Weakley (2005) also lists a ruderal habitat with 264 native taxa and the habitat for 41 species was not determined, but given that no rare species within the Southeast including the Carolinas fell within these categories, they were omitted (see Appendix II for habitat delimiting criteria).

To get a general sense of species distributions across habitat types, this characterization was first extrapolated to the entire coverage area and each species was assigned to a single habitat type (Table 2.2). Because even rare species occupy a range of habitat types, the four general habitat categories listed in Table 2.2 allow for a broad yet meaningful analysis of environmental association patterns. For example, *Malaxis bayardii* (Bayard's adder's-mouth orchid) occurs across a variety of habitats, including dry, open upland forests and shale barrens (Weakley, 2006) and was therefore scored under the more broad “General woodlands and glades” category. This particular analysis, however, is not absolute and several species many not fit into any category particularly well. Nevertheless, it does broadly and quantitatively illustrate which habitats harbor exceptional numbers of rare species.

To ascertain which habitats contain high numbers of rare species, a linear regression of the number of rare species vs. the number of native species per habitat was carried out for North and South Carolina native plants only. Representative natural areas in the Carolinas for each habitat type are also listed (Table 2.2).

How is rarity distributed among taxonomic groups?

Several authors have investigated whether rare species are randomly distributed across taxa and evidence indicates that rare species are clustered within certain groups (Schwartz, 1993; Edwards, 1998; Schwartz and Simberloff, 2001; Pilgrim et al., 2004; Domínquez Lozano and Schwartz, 2005). Studies suggest that patterns in rarity at the family level accurately reflect patterns at lower taxonomic levels (Edwards, 1998). As a result, I chose the family level to investigate patterns in the taxonomic distribution of rarity within the Southeastern flora. To test the null hypothesis that rarity is independent of taxonomic group size, a linear regression of the number of rare species vs. family size for the Southeast was used.

Data analysis

All statistical analyses were performed using S-PLUS version 7.0 (Insightful Corp., Seattle, WA). Residual diagnostic analyses were performed to test the robustness of linear regression models and to assess trends in residuals. Residual plots were also used to identify the largest deviations from the model. Cook's residual distance measure was used to test whether particular observations are heavily influential or statistically significant outliers. Species area relations were log or semi-log transformed for ecoregional analyses.

Results

How are rare species distributed in the Southeast?

At the state level, the highest concentration of rare and federally listed plant species occur in Georgia (Table 2.3). Of rare species, Alabama had the highest proportion of endemics (20%), followed by northeastern and Panhandle Florida (19%). At the ecoregional scale, rare species diversity was greatest in Southeastern Conifer forests followed by Appalachian/Blue Ridge Forests (Table 2.1). Middle Atlantic Coastal Forests ranked third in terms of species numbers, indicating that the ecoregions of the Southeastern Coastal Plain are exceptionally high in species diversity.

With respect to the effect of area on rare plant diversity, linear regressions were positive and significant for nearly all ecoregions analyzed (Fig. 2.2), including Appalachian/Blue Ridge Forests ($n = 105$, $r^2 = 0.09$, $P = 0.002$), Appalachian Mixed Mesophytic Forests ($n = 45$, $r^2 = 0.18$, $P = 0.003$), Central U.S. Hardwood Forests ($n = 50$, $r^2 = 0.12$, $P = 0.01$), Middle Atlantic Coastal Forests ($n = 71$, $r^2 = 0.16$, $P < 0.001$), and Southeastern Conifer Forests ($n = 124$, $r^2 = 0.04$, $P = 0.02$). The species area relationship for Southeastern Mixed Forests, however, was not statistically significant no matter which data transformation was used ($n = 137$, $r^2 < 0.001$, $P = 0.87$). Although all regressions were highly significant, the total amount of variation explained was relatively small, suggesting the influence of other factors on rare plant diversity not tested here. Upon closer inspection, however, there were several counties for each ecoregion that contained more species than expected (Table 2.4). While many counties had high, positive deviations from linear models, the counties listed in Table 2.4 were found to be exceptionally rich in rare species and represent the highest squared residual deviations in linear regressions. These particular counties roughly correspond to the Apalachicola region of the Florida Panhandle, outer coastal plain of North Carolina, the southern portion of the Blue Ridge and Cumberland Plateau, and the Central Basin of Tennessee.

Are rare plants clustered within particular habitat types?

Nearly half (46%) of all Southeastern rare plants occur in woodland and glade habitats, of which 25% are limited to calcareous glades, woodlands, or prairies, and 21% to dry pinelands (Table 2.3). Upland forested habitats contain 49 rare species (22% of total), a large proportion of which (31%) are restricted to lowland mesic forests. Similar species numbers were recorded for bottomland and alluvial habitats and saturated boggy habitats (26 species each) as well as rock outcrop and miscellaneous habitats (13 and 10).

The relationship between the number of species per habitat vs. the number of rare species for the Carolinas was positive and significant ($n = 33$, $r^2 = 0.25$, $P < 0.01$), indicating that the number of rare species among habitat types is strongly correlated with species diversity in general. The amount of variation explained by the relationship, however, is also relatively low and suggests the significance of other factors correlated with rare species distribution among habitat types. Several habitats for the Carolinas were poorly predicted by the linear model. In particular, Coastal Plain blackwater bottomlands, wet pinelands, and mafic glades woodlands and prairies were over-represented in rare species while general woodlands and glades, and general wet acidic situations were under-represented.

How is rarity distributed among taxonomic groups?

A total of 69 plant families and 145 genera are represented among rare Southeastern plants. Well-represented genera were *Isoetes* and *Carex*, with 10 and 8 species each. Rare species frequency distribution across families in the Southeastern U.S. were strongly skewed

(Fig. 2.4). About 86 % of families had less than three rare species; the majority (49%) had only one rare species recorded for the Southeast. Stacked histograms of the number of rare species per the number of total native species in plant families show that while larger families typically have more rare species, the relative proportion of rare species is repeatedly higher in smaller families (Fig 2.5). This is especially evident in the Isoetaceae, where the number of rare species is conspicuously high compared to other families of equivalent size.

Cook's distance plots revealed three significantly influential outliers for the number of rare species vs. the total number of species per family for the Southeast: Asteraceae (593 spp, 39 rare); Cyperaceae (495 spp, 17 rare); and Poaceae (403 spp, 8 rare). These outliers were removed to improve resolution among the less species rich families. The latter two families had fewer rare species than initially predicted by the model. Although the total amount of variation explained by regression was slightly higher prior to omitting the outliers ($n = 69$, $r^2 = 0.77$, $P = 0.00$), the relationship was remarkably significant ($n = 66$, $r^2 = 0.59$, $P < 0.0001$) and most large families fall outside 95% confidence intervals for expected numbers of rare species. A scatter diagram of the number of rare species per family size illustrates two families that strongly deviated from the linear relationship: Isoetaceae and Brassicaceae with 0.38 and 0.14 proportion rare (Fig. 2.6). A complete list of plant families, inclusive species, and geographic range are recorded in Appendix II.

Discussion

Phytogeography and plant ecology of rarity

Examining species distribution patterns at the state level is broadly useful for identifying conservation targets. State-based assessments and the establishment of rare lists are used in inventory, establishing formal legal protection, and frequently form the basis of conservation planning. The list of globally rare imperiled plant species reported here are consistent with state patterns of endemism or imperilment observed elsewhere (Dobson et al., 1997; Estill and Cruzan, 2001; Chaplin et al, 2001; Stein et al., 2001), suggesting that at most spatial scales, areas rich in endemism and rare species are associated with site-specific evolutionary patterns and process and unique habitats (Stohlgren et al., 2005). Although it is beyond the scope of this study to examine every ecoregion in detail, I do give a brief overview of the distinguishing features for those ecoregions especially rich in rare species and the habitats in which they occur.

Appalachian/Blue Ridge Forests and Appalachian Mixed Mesophytic Forests

Southeastern ecoregions consistently rank among the most diverse both in terms of species richness and rare plant composition, particularly the Appalachian/Blue Ridge Forests ecoregion. Geologic stability, geographic and genetic isolation, disturbance, and variation in topography and physiography have all led to a unique and rich assemblage of plants and is arguably the most primitive flora in the world (White, 1984; Delcourt and Delcourt, 1998; Kartesz and Farstad, 1999). In conjunction with Appalachian Mixed Mesophytic Forests, Appalachian/Blue Ridge forests contain the highest amount of endemic flora in North America (Stephenson et al., 1993; Ricketts et al., 1999b). In this study, slightly less than 30% of all Southeastern rare taxa are endemic to these two ecoregions. Many of these species are relicts of an alpine or tundra flora following interglacial warming (White, 1984) that have persisted in open, stable habitats. The majority of rare Appalachian plants (~ 44%) occur in woodland and glade habitats, particularly calcareous glades, woodlands, and prairies. Bibb County, Alabama, located at the extreme southern end of the Ridge and Valley physiographic province, falls out as an unexpectedly rich county in rare species. A botanical "lost world" (Allison and Stevens, 2001), many species occur in "Ketona" glades recently described by Allison (1994) and Allison and Stevens (2001). The unusual pure dolomite that constitutes the Ketona Formation is unique to Bibb County. According to Baskin and Baskin (2003), the Ketona glades of Bibb County are not true cedar glades which are dominated by poverty dropseed (*Sporobolus vaginiflorus*) and infrequently found in the little bluestem (*Schizachyrium scoparium*) dominated Ketona dolomite outcrops. The high concentration of rare plants in Bibb County may also be partly a result of newly split species, particularly in difficult genera such as *Carex* and *Isoetes* (Allison and Stevens, 2001). Similarly, of the eight species reported for DeKalb County, AL six occur in glade habitats.

In spite of their infrequent occurrence, high elevation rock outcrop communities in the Southern Appalachians also harbor high numbers of rare species that occur in few other habitats in the region (Miller, 1986; Baskin and Baskin, 1988; Johnson, 1996; Wiser et al., 1996; 1998). Wiser and others (1998) demonstrate the importance of site-scale parameters such as potential solar radiation and soil-nutrient gradients in predicting rare species distributions among high elevation rock outcrops. Similarly, Miller (1986) found elevation diversity to be the best predictor of rare species richness, especially in Great Smoky Mountains National Park. Other important rare plant habitats in the Southern Appalachians include montane seepy habitats such as bogs (Pittillo, 1984) and other nonalluvial wetlands (Murdock, 1994; Warren et al., 2004) as well upland forested habitats, which contained approximately 25% of montane species.

Middle Atlantic Coastal Forests and Southeastern Conifer Forests

The Southeastern Conifer forests that span the coastal plain of Georgia, the Florida Panhandle, Alabama and Mississippi rank highest in terms of tree diversity and endemism (Ricketts et al., 1999b; Estill and Cruzan, 2001). Specifically, fire-maintained longleaf pine (*Pinus palustris*) and wiregrass (*Aristida stricta*) communities contain some of the richest herbaceous flora in the world (Noss and Peters, 1995) and some of the highest levels of endemism in North America and the Southeast (Estill and Cruzan, 2001). Here, more than one quarter of rare plants in the Southeast are restricted to this ecoregion. With the exception of the Florida Panhandle and a few other areas, Southeastern Conifer Forests lack isolating factors (e.g. mountains, isolated habitats) frequently associated with endemism (Kartesz and Farstad, 1999). In contrast, large geographic extent, abundance of moisture, and intense light levels may be responsible for producing the rich flora and endemics observed in this region.

The most species rich counties (including Liberty and Bay counties, FL), not only in the Coastal Plain but in the entire Southeast, occur in the Apalachicola region of the Florida Panhandle. The species diversity observed for the Southeastern Coastal Plain is likely due to the high incidence of rare species in these counties. The vegetation of the Panhandle consists of mixed-hardwood hammocks where rare species such as the Florida Torreya (*Torreya taxifolia*) and the Florida yew (*Taxus floridana*) persist on protected bluffs along the Apalachicola River. Other major vegetation types include more open *Pinus palustris* dominated sandhills, savannas and flatwoods; the species richness of these habitats is well-documented here and elsewhere (Walker, 1993; Gray, 2003). Again, woodland and glade habitats are especially rich in rare species, containing roughly 40% of all rare plants in the Coastal Plain province; most of these species (85%) are distributed among wet and dry pinelands. Nearly 20% of Southeastern Coastal Plain rare plants, however, occur in bottomland and alluvial habitats as well as saturated boggy habitats. Coastal Plain blackwater bottomlands in particular had more rare species than predicted by linear regression for the Carolinas. Rare species richness was also high in Coastal Plain natural ponds and depression meadows. Vegetation composition and dynamics in these habitats are principally controlled by hydrologic processes (Edwards and Weakley, 2001) and spatial and temporal variation in water level influences species composition along hydrologic gradients.

Central U.S. Hardwood Forests

Broadleaf deciduous trees dominate the Central Hardwood Forest ecoregion, which is one of the most diverse in North America for herbaceous plants and shrubs (Ricketts et al., 1999b). However, approximately 75% of rare plant species in this ecoregion occur in glade habitats. Most (80%) of the rare plants located in the most species rich counties of the Central Basin of Tennessee are associated with woodland and glade habitats. Of these, 75% are associated with calcareous substrates or "cedar glades"; high levels of endemism and near-endemism in Southeastern cedar glades are well known (Kral, 1973; Baskin and Baskin, 1999; 2003). These habitats, usually dominated by herbaceous species, are characterized by limestone or dolomite rock outcroppings over shallow soils and are located in Tennessee, Kentucky, and northern Alabama (Baskin and Baskin, 1999). Other distinguishing features include high irradiance, extreme variation in soil moisture and high soil temperatures in the summer. According to Weakley (2005), the clustering of rare species in woodland and glade habitats is largely attributed to distinct, specialized substrates (e.g. calcareous, serpentine, and mafic rocks). Furthermore, the open nature of these provides ideal conditions for sun-loving upland taxa. As a result, several disjunct taxa with specific ecological requirements are frequently found in these habitats. Habitat specialization likely accounts for the under-representation of rare plants in general habitat categories.

Taxonomic patterns of rarity

In plants, evidence suggests that smaller taxonomic groups consistently contain fewer than expected numbers of rare species (Schwartz and Simberloff, 2001; Pilgrim et al., 2004; Domínguez Lozano and Schwartz, 2005). Recent studies have demonstrated that unlike other taxonomic groups, small plant families consistently contain fewer rare plant species than expected while rare plants are proportionately over-represented in larger families (Schwartz and Simberloff, 2001; Domínguez Lozano and Schwartz, 2005). In the Southeast, rarity was not evenly distributed among plant families and corroborates previous findings. Schwartz and Simberloff (2001) suggest that differential rates of speciation and extinction among families may be correlated with rarity and high speciation in large groups, for example, is associated with high rates of rarity. Alternatively, groups that experience high rates of extinction are likely to lose their rare species first, leaving the more common congeners as the remaining representatives of smaller lineages (Schwartz and Simberloff, 2001). Another explanation for these patterns may be due to differences in taxonomic treatment (Schwartz and Simberloff, 2001), which can artificially inflate rare species lists (Isaac et al., 2004). The over-representation of Isoetaceae, for example, may be a result of taxonomic splitting. The reliance on threatened species lists is fundamental to conservation and priority setting. A recent study, however, showed that hotspots of endemism shift spatially with changing species concepts (Peterson and Navarro-Siguenza, 1999), indicating that hotspots are not permanent features on the landscape.

Nonetheless, the conservation implication of the findings presented in this paper suggests two somewhat contrasting strategies. First, if capturing phylogenetic diversity is the conservation objective (see Rodrigues and Gaston, 2002) then attention might be directed towards those groups with the highest number of rare species, particularly if the diversity of lineages is greatest in these groups due to high rates of speciation. In contrast, taxonomic distinctiveness is not limited to the boundaries of any particular family, suggesting that conservation should maximize the number of families with higher rates of rarity. For instance, there is only one native species in the Southeast representing the Illiaceae family, *Illicium parviflorum*, which is globally rare and restricted to two states. Loss of the species means loss of the lineage. This is true for several families with relatively high proportions of rare species, including Taxaceae, Diapensiaceae, Calycanthaceae and Loganiaceae.

It is important to note, however, that there is no consistency across regions or continents as to which families will have more or less rare species (Edwards and Westoby, 2000) and conservation of particular groups will have to be context-dependent. And, while the identification of areas for conservation must balance the needs of multiple taxa, given that inventory data for vascular plants is more complete than other taxonomic groups, measures of species richness based on plant data will continue to guide conservation planning.

Figures

Figure 2.1 Geographic area of analysis for the Southeastern U.S., including state and ecoregional boundaries.

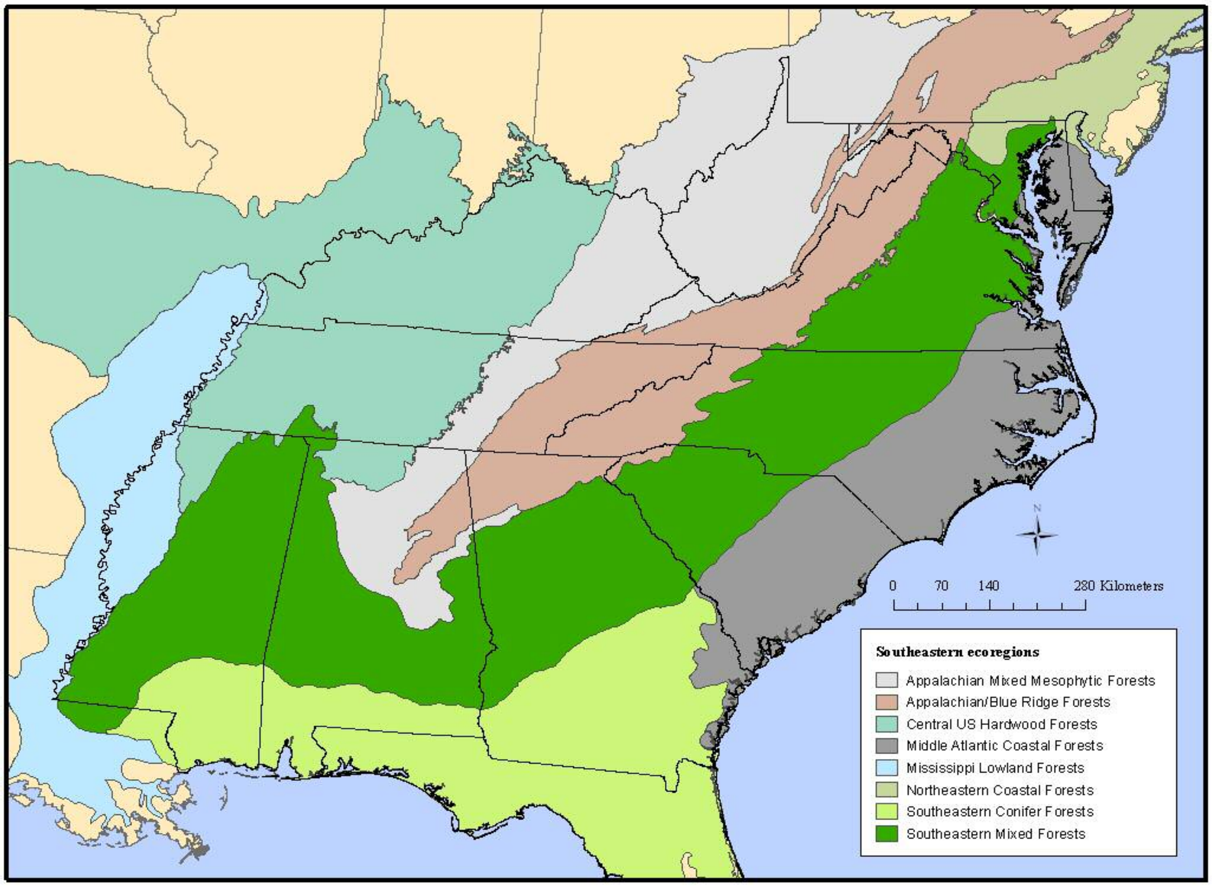


Figure 2.2 Scatter diagrams for the number of species per county area for: (A) Southeastern Conifer Forests; (B) Middle Atlantic Coastal Forests; (C) Appalachian/Blue Ridge Forests (D) Appalachian Mixed Mesophytic Forests; and (E) Central US Hardwood Forests. Solid lines indicate a linear fit and dashed lines represent 95% confidence intervals.

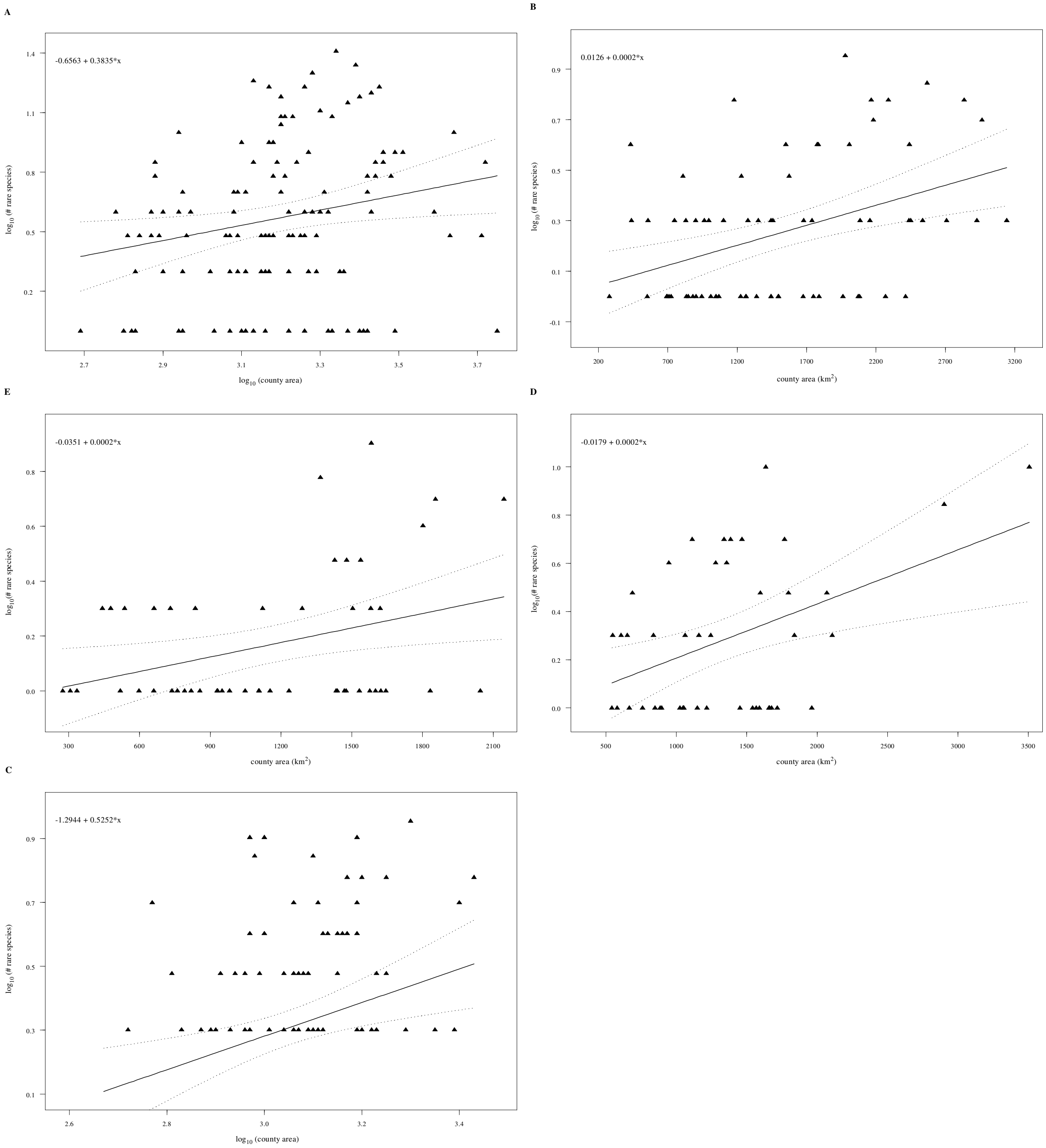


Figure 2.3 A scatter diagram for the number of rare species per habitat type in the Carolinas (n = 33). Solid line indicates a linear fit and dashed lines represent the 95% confidence interval.

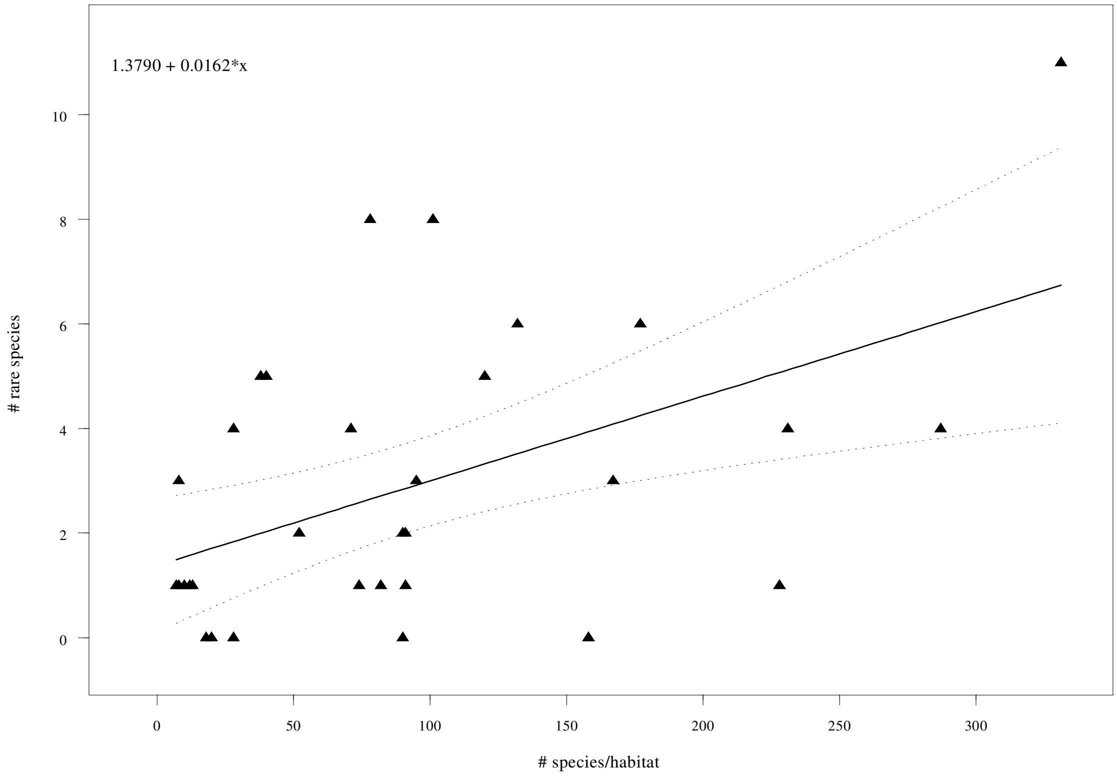


Figure 2.4 A frequency histogram of the number of rare plants per plant family for the Southeast (n = 70) is strongly skewed to the right. Most families (86%) have 3 or fewer rare species.

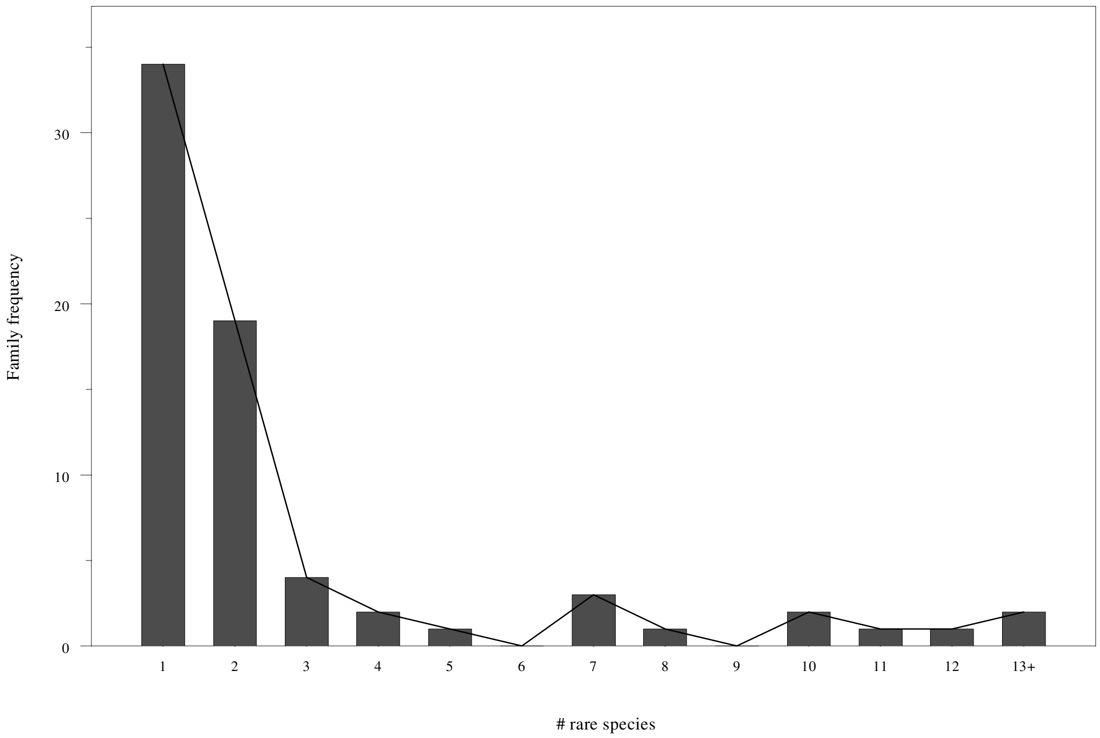


Figure 2.5 Stacked histograms of distribution of rare species among plant families for the Southeast. The height of the bottom segment in each stack is the number of rare species and the height of the top segment is the number of total native species per plant family. Families are listed in increasing size. While larger families typically have more rare species, the relative proportion of rare species is repeatedly higher in smaller families.

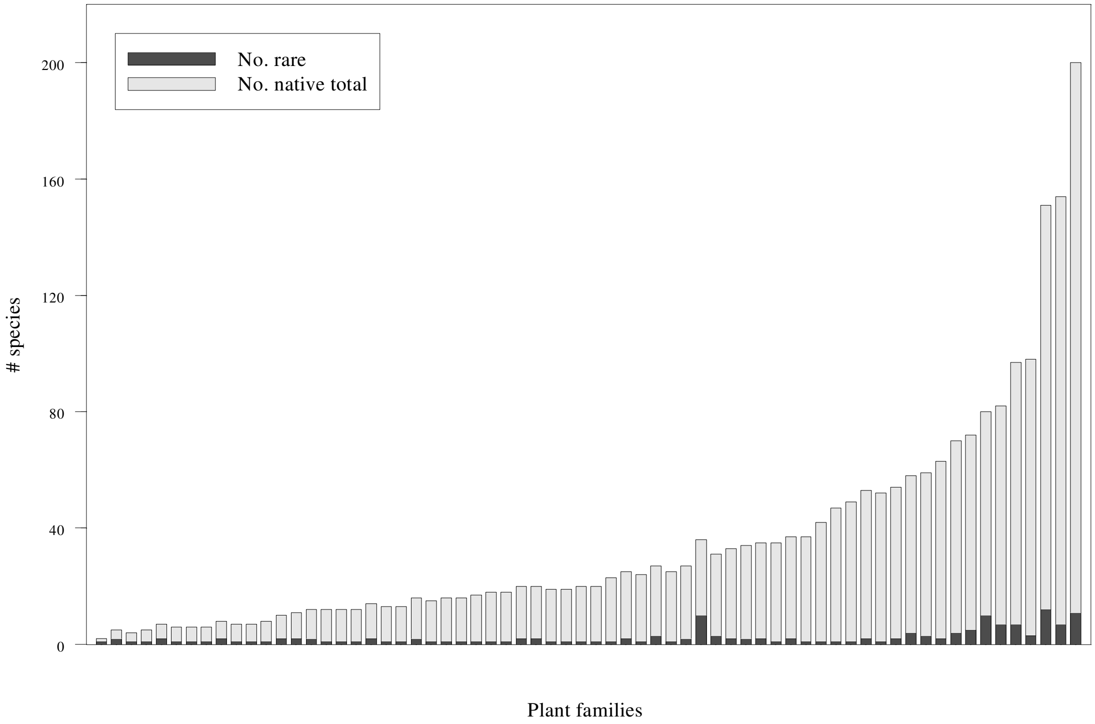
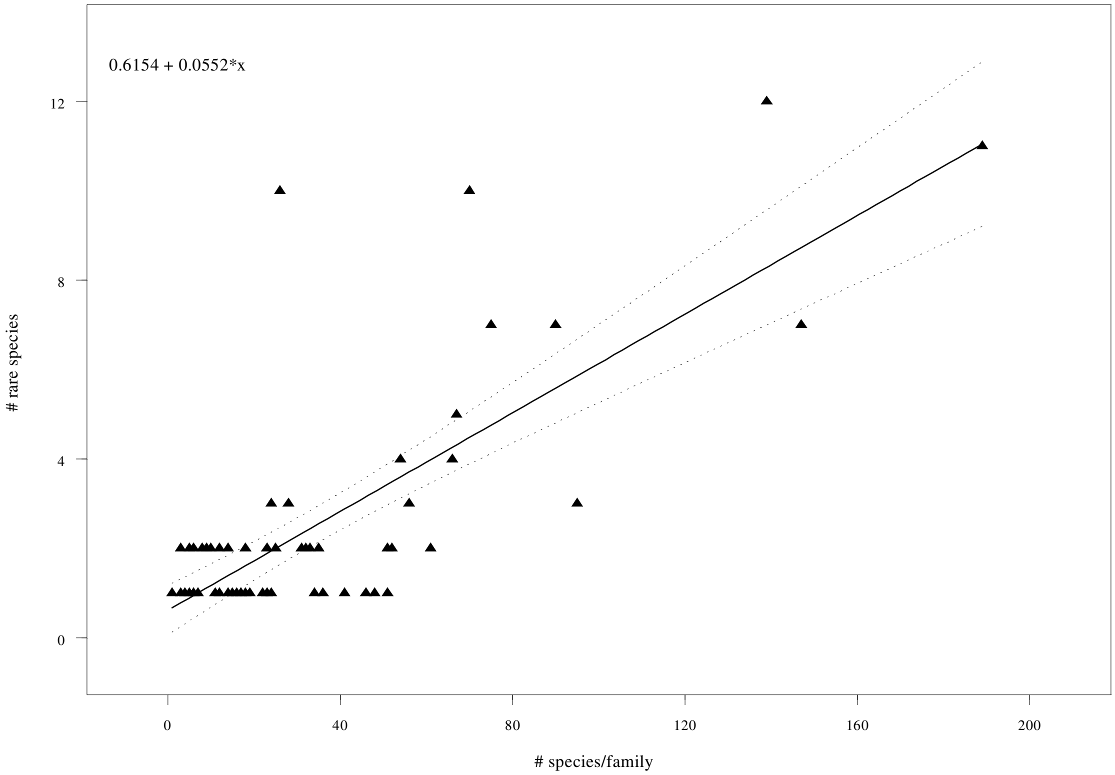


Figure 2.6 A scatter diagram for the number of rare species per family size in the Southeast. Three extreme outliers were removed for improved resolution: Asteraceae, Cyperaceae, and Poaceae. Solid line indicates a linear fit and dashed lines represent the 95% confidence interval.



Tables

Table 2.1 Rare species diversity among Southeastern terrestrial ecoregions.

Ecoregion	Area (km^2)	# plant spp	# rare spp
Northeastern Coastal Forests	89691	1695	5
Appalachian/Blue Ridge Forests	159266	2398	78
Appalachian Mixed Mesophytic Forests	18300	2487	60
Central U.S. Hardwood Forests	296019	2332	24
Mississippi Lowland Forests	112284	1468	1
Southeast Mixed Forests	347803	3363	57
Middle Atlantic Coastal Forests	133855	1488	52
Southeast Conifer Forests	236759	3095	98

Table 2.2 The number of rare and native plants found in Southeastern habitats defined by Weakley (2005). Representative natural areas are listed for the Carolinas (after Schafale and Weakley, 1990).

Habitat Category	**Representative areas**	**# rare spp (Southeast)**	**# spp (NC, SC)**	**# rare spp (NC, SC)**
UPLAND FORESTED HABITATS				
High elevation forests	Mt. Mitchell State Park	2	90	2
Acid cove	Great Smoky Mountains NP	4	28	4
Rich cove	Station Cove, Sumter NF	5	167	3
Montane dry forest	Uwharrie National Forest	3	91	2
Lowland mesic forest	W.B. Umstead State Park	15	177	6
Lowland acid dry forest	Hanging Rock State Park	3	90	0
Lowland calcareous dry forest	Hunters Creek Forest, Croatan NF	8	7	1
Coastal Plain hammock	Cape Hatteras National Seashore	5	40	5
General upland forest		3	91	1
BOTTOMLAND AND ALLUVIAL HABITATS				
CP blackwater bottomlands	Four Holes Swamp	13	78	8
Brownwater bottomlands	Roanoke River	1	20	0
CP calcareous wet flats and bottoms	Rocky Point Marl Forest	3	28	0
General bottomlands		6	287	4
WOODLAND AND GLADE HABITATS				
High elevation glades and woodlands	Big Bald Natural Area	1	13	1
Granite glades and woodlands	Stone Mountain	9	71	4
Mafic glades, woodlands, and prairies	McDowell Nature Preserve	7	101	8
Calcareous glades, woodlands, and prairies	Catawba River Dolomite Area	26	12	1
Shale glades, woodlands, and prairies	Buck Creek Serpentine Barren	5	8	1
Riverside scour glades	Eno River State Park	7	8	3
Dry pinelands (Sandhills)	Sandy Island	18	231	4
Wet pinelands (Savannas and Flatwoods)	Green Swamp Preserve	22	331	11
General woodlands and glades		9	228	1
SATURATED BOGGY HABITATS				
CP natural ponds and depression meadows	Tunstall's Bay, Scotland County	12	120	5
CP pocosins	Francis Marion NF	2	52	2
Montane fens, seeps, depressions	Bluff Mountain Preserve	8	132	6
General wet acidic situations		4	158	0
ROCK OUTCROP HABITATS				
High elevation summit outcrops	Grandfather Mountain	6	38	5
Acid outcrops	Hemlock Bluffs	5	18	0
Calcareous outcrops	Linville Caverns	1	20	0
Montane waterfall spray cliffs	Schoolhouse Falls, Panthertown	1	10	1
MISCELLANEOUS HABITATS				
Barrier island beaches, dunes, depressions	Botany Bay Island	2	74	1
Aquatic	Washo Reserve	5	82	1
Tidal	Winyah Bay	3	95	3
TOTAL		224	2996	94

Table 2.3 State occurrences of rare, endemic, and federally listed vascular plant species. The total number of species data is from Stein et al. (2000). Extirpated species were excluded from analysis. Federally listed rare species include Endangered, Threatened, and Candidate species.

State	Total # species	# rare	# endemic	# federally listed
Georgia	2986	112	13	26
Alabama	2851	87	17	18
North Carolina	2743	78	8	22
Florida	2995	74	14	12
South Carolina	2543	54	2	17
Virginia	2546	41	3	10
Tennessee	2376	47	7	16
West Virginia	1876	18	1	5
Mississippi	2314	20	0	3
Kentucky	2050	15	2	8
Maryland	2226	16	1	4
Delaware	1669	8	1	4
DC	1287	2	0	0

Table 2.4 Counties with exceptional rare floras within Southeastern terrestrial ecoregions. These counties represent the highest squared residual deviations in linear regressions for the number of rare species vs. county area.

Ecoregion	**County**	**County area (km^2)**	**# rare spp**
Southeastern Conifer Forests	Liberty Co., FL	2208	26
	Bay Co., FL	1910	20
	Gadsen Co., FL	1345	18
Middle Atlantic Coastal Forests	Onslow Co., NC	1979	9
	New Castle Co., DE	1178	6
	New Hanover Co., NC	431	4
Appalachian/Blue Ridge Forests	Carter Co., TN	934	8
	Henderson Co., NC	962	7
	Rabun Co., GA	968	8
Appalachian Mixed Mesophytic Forests	Bibb Co., AL	1635	10
	McCreary Co., KY	1113	5
	Morgan, Co., TN	1339	5
Central US Hardwood Forests	Rutherford Co., TN	1583	8
	Davidson Co., TN	1367	6

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III. CONSERVATION IMPLICATIONS OF MATING SYSTEMS, FLORAL PHENOLOGY, AND SEXUAL EXPRESSION IN THE FEDERALLY ENDANGERED *PTILIMNIUM NODOSUM* (APIACEAE)

Abstract

Knowledge of plant mating system attributes is essential to the conservation of endangered species. The purpose of this study was to examine the functional consequences of protandry, andromonoecy, and mating patterns in the critically endangered and clonal plant, *Ptilimnium nodosum*. I conducted intra- and interfloral phenological observations to quantify opportunities for geitonogamy and calculated floral sex ratios of sequentially blooming umbel orders. I also provide information on *P. nodosum*'s mating system. Flowers are self-compatible, but strong intrafloral dichogamy precludes autogamous selfing (<1% seed set). Weak interfloral dichogamy combined with vegetative reproduction, however, provides multiple opportunities for geitonogamy which characteristically decrease with umbel order. Although low, mean seed set was comparable among open-pollinated (25%), manually outcrossed (26%), and geitonogamously selfed (21%) pollination treatments, indicating a mixed-mating system dependent on insect-mediated pollination.

The significant decrease in mean seed set observed among higher umbel orders in open-pollinated plants is likely a consequence of low floral density and lack of pollinators late in the flowering season. Moderate reproductive output and high seed germinability suggests that environmental conditions, not breeding system, regulate the distribution and

abundance of *P. nodosum* and high immediate fitness gained by vegetative reproduction plays a critical role to species' the short-term persistence.

Introduction

The collection of relevant biological information is critical to establishing recovery criteria for endangered species. The lack of basic biological data has been implicated in the failure of numerous species recovery plans, especially for rare plants (Gottlieb, 1991; Holsinger and Pavlik, 1994; Schemske et al., 1994; Boersma et al., 2001; Schultz and Gerber, 2002; Heywood and Iriondo, 2003). Knowledge of plant mating systems is critical to the effective management of rare and endangered species (Hamrick et al., 1991; Karron, 1991; DeMauro, 1993; Weller, 1994). Differences in mating patterns can influence the amount and distribution of genetic diversity within a species as well as a population's effective size (Simberloff, 1988; Lande, 1993; Holsinger, 2000). The effects of random stochastic forces are exceptionally acute in small, genetically isolated populations, and they may increase a species' probability of extinction (Barrett and Kohn, 1991; Young et al., 1996). Similarly, genetic drift, inbreeding, and mutation accumulation increase in finite populations, all of which can affect the evolutionary potential of a species to adapt to a changing environment via natural selection (Lynch et al., 1995; Holsinger, 2000).

In general, outcrossed progeny demonstrate higher levels of genetic diversity than those produced by self-fertilization, which are expected to drift toward genetic uniformity. Consequently, selfers are presumed to be less fit than outcrossing individuals due to the effects of inbreeding depression and the accumulation of deleterious, recessive alleles (Rollins, 1967; Schemske and Lande, 1985; Lloyd and Webb, 1986; Charlesworth and

Charlesworth, 1987; Lloyd, 1992). Nonetheless, in a highly selfing population, these alleles will be expunged and selfed progeny may not demonstrate signs of inbreeding depression. Furthermore, selfing provides a selective advantage by ensuring reproductive success when pollen transfer is limited and a self-compatible individual acts as both pollen and ovule parent to its offspring (Fisher, 1941; Stebbins, 1957; Jain, 1976; Schoen et al., 1996; Holsinger, 2000).

There are several floral features that influence plant mating systems and the extent to which a species is outcrossing or selfing. The temporal separation of pollen presentation and stigma receptivity (dichogamy), floral architecture, and the production of separate male flowers (andromonecy) all have the effect of reducing intrafloral self-pollination (Charlesworth and Charlesworth, 1987; van Treuren et al., 1993; Freeman et al., 1997). These mechanisms for avoiding inbreeding are especially evident in the Apiaceae (subfamily Apioideae), a family remarkably homogeneous in floral characteristics. In addition to morphological uniformity in flowers, fruits, and inflorescences, most taxa are cosexual and self-compatible (Webb, 1981). Selfing is common in apioid umbellifers where large numbers of small flowers arranged in tightly clustered compound umbels are likely to come in contact, yet the widespread existence of dichogamy indicates a mechanism for outcrossing (Ponomarev, 1960; Bell, 1971; Cruden and Hermann-Parker, 1977; Webb, 1981; Lindsey, 1982; Lloyd and Webb, 1986; Schlessman and Graceffa, 2001; Schlessman and Barrie, 2004). The rate of outcrossing, however, depends in part on the strength of dichogamy and sexual expression patterns. Protandry, where pollen presentation precedes stigma receptivity, is a form of dichogamy common in apioid taxa and occurs at three structural levels: within a single flower (intrafloral protandry); between flowers on the same umbel; and among umbels of different orders (interfloral protandry). Obligate outcrossing will only be imposed if protandry is strong enough to preclude selfing and the overlap of sexual functions (Bell, 1971).

In addition, andromonoecious taxa produce both perfect and staminate flowers, the latter having functional stamens but lacking developed ovaries. The proportion of staminate flowers characteristically increases with higher umbel orders in protandrous apioid taxa and can influence fruit set and outcrossing patterns among flowers (Bell, 1971; Lovett Doust, 1980; Webb, 1981; Lindsey, 1982; Koul et al., 1993; Brunet and Charlesworth, 1995; Schlessman and Graceffa, 2001). If, however, protandry is only weakly developed, then geitonogamy, or the transfer of pollen between flowers on the same plant, can occur if more than one flower within the same umbel, flowering branch, or clone is open at the same time. Although genetically equivalent to autogamy (within flower self-pollination), geitonogamy is not expected to provide reproductive assurance (Harder and Barrett, 1995; Barrett, 1998; Holsinger, 2000). Furthermore, because geitonogamy requires pollinator visitation, pollen export to other individuals may be reduced (pollen discounting) and lead to fewer successfully fertilized ovules by outcrossed pollen (seed discounting) (Holsinger et al., 1984; Lloyd, 1992; de Jong et al., 1993; Harder and Barrett, 1995; Schoen et al., 1996 Barrett, 1998; Eckert, 2000).

In this study, I examined the reproductive biology of *Ptilimnium nodosum* (Rose) Mathias, a federally endangered protandrous plant. While *P. nodosum* is assumed to share many of the floral traits characteristic of apioid taxa, the basic biology of the species is unknown. Specifically, to determine the significance of protandry in regulating self-fertilization in the species, I studied floral phenology patterns at three levels: (1) intrafloral and interfloral (2) within, and (3) among sequentially blooming compound umbels. I calculated differences in sex expression and seed set among umbel orders. I performed controlled crosses to determine the breeding system of *P. nodosum* and evaluated differences in seed set and germination rates among crossing treatments. Finally, I conclude with a discussion on the consequences of floral attributes in *P. nodosum* and the evolutionary significance of breeding systems to the conservation and persistence of the species.

Methods

Study species

Ptilimnium nodosum, commonly known as harperella, is a federally endangered, semi-aquatic perennial. Historically, *P. nodosum* was split into three separate species based on ecological differentiation. Two species (*P. viviparum* (Rose) Mathias and *P. fluviatile* (Rose) Mathias are riverine ecotypes that occur along gravel shoals in seasonally flooded rocky rivers in West Virginia, Maryland, Virginia, North Carolina, Alabama, and Arkansas. The pond ecotype, *P. nodosum* sensu stricto is limited to pond edges in South Carolina and Georgia. Genetic evidence does indicate differentiation among the three ecotypes (Kress et al., 1994), but the treatment of the species in this study as a single taxonomic entity, *P. nodosum* sensu lato, follows Kral (1981).

Ptilimnium nodosum typically grows between rocks and gravel of riverside scour glades, a habitat characterized by open, prairie-like conditions maintained by periodic flooding (Weakley, 2005). The species is restricted to a narrow range of water depths and depends on scouring from flood overwash to eliminate competition from encroaching woody vegetation. Between year variability in flooding is an important factor in restructuring geomorphic surfaces and regulating *P. nodosum* population dynamics. Populations are substructured into smaller units usually consisting of fewer than two hundred individuals and experience significant turnover (USFWS, 1990). Maddox (1991), for example, reports that as much as 10% of subpopulations in the Sideling Hill Creek, Maryland population disappear in a given year. More recently, two successive 500 year floods in the winter of 1996/1997 decimated two of the largest remaining populations of *P. nodosum* along the Cacapon River and Sleepy Creek in West Virginia. In 1988, an estimated 150,000 plants were originally surveyed in the Cacapon River population, but only five plants were found following flooding in the summer of 1997 (P. Harmon, West Virginia Department of Natural Resources, pers. comm.).

Kral (1981) suggested that the aquatic habitat may lead to the development of self-fertilization and, like other rare species, *P. nodosum* is genetically depauperate (Kress et al., 1994) with a capacity for vegetative reproduction and clonal spread. Fluctuating water levels can topple flowering stalks and induce vegetative growth along the nodes, producing independent ramets when flowering stalks die back. This phenomenon allows the species to anchor to substrates when plantlets are dislodged by erosive action and may facilitate establishment elsewhere. For instance, an “explosion” of plants was discovered in newly exposed bedrock within the stream channel following scouring from winter ice jams in West Virginia (P. Harmon, pers. comm.). Although the contribution of vegetative reproduction to the colonization of new sites is relatively unknown, new populations of *P. nodosum* have been discovered (see Belden, 2003).

Flowering occurs from July through late August. The flowering stalk is composed of compound umbels bearing small white, tightly spaced flowers; peduncles are terminal (primary, or first order) and axillary (secondary, tertiary, etc., or second, third orders). Floral development is from the periphery inward of an umbel (centripetal) and from the top down of a flowering stalk (basipetal). Like many of its congeners, *P. nodosum* is an andromonoecious and protandrous plant; the proportion of staminate flowers increases in higher umbel orders and male and female phases are temporally separated both between flowers and sequentially blooming umbel orders, yielding repeated cycles of protandry (Bell, 1971; Webb, 1981; Lloyd and Webb, 1986; Schlessman and Barrie, 2004). Following flower opening, anthers split longitudinally and dehisce in succession over a period of several days until stigmas become receptive.

Sampling

Historically known from 26 locations across six states (West Virginia, Maryland, North Carolina, Alabama, Arkansas, and more recently Virginia), *P. nodosum* is currently restricted to 13 remaining populations. In North Carolina, biogeographic records confirmed three populations of which only one, consisting of 100-150 individuals, remains today along the Tar River in Granville County. Two additional populations previously occurred along the Deep River at the intersection of Chatham and Lee Counties, but due to severe reductions in population size the remaining individuals were rescued and transplanted to the North Carolina Botanical Garden in Chapel Hill where all experiments and observations were carried out.

Floral phenology and sex expression

The floral phenology for 30 randomly chosen individuals was recorded daily from 16 June through 7 August 2006. During each observation, perfect flowers were scored into five phenological stages: bud closed (stage 1); flower opening (stage 2); anthesis (stage 3);

filaments recumbent, styles elongating (stage 4); and stigmas spreading, secretions evident (stage 5). These stages of protandrous development approximate those used by Lindsey (1982) to describe protogynous floral phenology patterns in *Thaspium* and *Zizia*. Excluding damaged umbels, all umbel orders were scored for each plant and a total of 28 first, 30 second, 24 third and 15 fourth order umbels were observed. The relative proportion of flowers in each stage per day was calculated and averaged across all umbel orders. Similarly, for all individuals observed in this study I counted the number of flowers in the female phase (stage 5) that were open simultaneously with flowers in the male phase (stage 3) divided by the total number of perfect flowers that enter the female phase. Values ranged from zero to 1.0, signifying absolute asynchrony to simultaneous expression of sexual phases. This calculation corresponds to that used by Dudash and Fenster (2001) who quantified geitonogamous selfing in *Silene virginica*; here, this measure was averaged across all umbel orders. These data allowed me to determine the strength of interfloral protandry within an individual. When overlap occurred, I calculated the ratio of flowers in the male phase to those of flowers in the female phase in order to estimate the contribution of each sexual function to potential geitonogamous pollinations.

Opportunities for geitonogamy within a flowering stalk were determined by calculating overlap in male and female phases between umbel orders. For geitonogamy to occur, one flower must be in anthesis during the same period that stigmas from a flower of a preceding umbel order are receptive. Specifically, synchrony in sexual phases was calculated by dividing the number of times sexual phases overlapped divided by the total number of umbels in the preceding order. While geitonogamy within a flowering stalk can also occur between stigma and pollen presentation by different flowers among umbels of the same order, this overlap was not documented in this study. Opportunities for geitonogamy between flowering stalks of the same plant were determined by scoring plants out of 100 randomly selected individuals that contained more than one stalk. These individuals were selected separate from mating system and phenological experiments.

We estimated floral sex ratios by scoring flowers as either perfect or staminate for each umbel order and the relative proportion of each flower type was documented. Perfect flowers where styles failed to elongate and mature were considered functionally staminate (Webb, 1981) and therefore scored as a staminate flower.

Mating systems

To determine *P. nodosum*'s mating system, I performed five pollination treatments in summer 2006 (Table 3.1). I documented the timing and duration of approximate stigma receptivity by randomly selecting 20 individuals and treating stigmas of different ages (measured in days) with a 3% hydrogen peroxide solution. Stigmas were classified as receptive based on the presence of bubbling, indicating peroxidase activity (Kearns and Inouye, 1993). All tests were observed under 10x magnification.

Eighteen individuals were randomly selected for each treatment excluding the control, which had a sample size of 22. In all crosses except the control, individuals were placed in pollinator exclusion tents constructed of white nylon, no-see-um netting enclosed over a polyvinyl chloride (PVC) frame. Under the assumption that *P. nodosum* is self-compatible, I caged plants prior to flower opening and sprayed them with pyrethrin oil to kill thrips, a 'universal pollinator' which often infest and self-pollinate apioid umbels (Bell, 1971).

Ptilimnium nodosum flowers are small and difficult to manipulate; therefore all treatments were integrated across an entire umbel rather than a sub-sample of flowers. To prevent any bias associated with umbel order, I chose among primary, secondary, and tertiary umbels for each pollination treatment. Few plants produced quaternary umbels, which were excluded from hand-pollination treatments. In addition, since emasculation is invasive and damaging, I occluded anthers with lanolin under a dissecting microscope in the manual outcrossing and geitonogamous selfing treatments. Pollen was collected from dehiscing anthers using separate toothpicks and transferred to receptive stigmas in all hand-pollination experiments (Kearns and Inouye, 1993). Since flower development is centripetal within an umbel, I repeated hand-pollinations over 2-3 days until all stigmas had darkened and begun to wilt.

Fruits were collected prior to dispersal and aborted or unfertilized fruits were discarded. Seed set was calculated for each umbel by dividing the number of viable seeds produced by the total number of ovules, and was averaged for each treatment. Variation in seed set was compared among primary, secondary and tertiary umbel orders of naturally outcrossing individuals.

Germination rate

Following collection, seeds were stored at room temperature for four weeks. The natural selfing treatment was omitted from germination studies due to low seed production (<20 seeds). One hundred seeds were treated in the open pollinated, manual outcrossing, and geitonogamy treatments and 25 in the manual selfing treatment, again due to low seed production. In order to break physiological dormancy, seeds from each pollination treatment were rinsed with a 1% bleach solution (C. Baskin, pers. comm.) and sown in a 50:50 seed starter and gravel media. Seed flats were then cold stratified at 42^{o}F for six weeks prior to being transferred to greenhouse conditions. The percentage of seeds germinated was compared across all treatments.

Data analysis

All statistical analyses were performed using S-PLUS version 7.0 (Insightful Corp., Seattle, WA). Shapiro-Wilk tests indicated lack of normality in the data: $W = 0.2098$, $P<0.001$; $W = 0.945$, $P<0.05$; and $W = 0.8678$, $P<0.001$ for floral sex ratios, seed set among umbel orders, and breeding systems data sets. However, because transformation could not meet the assumptions required for ANOVA, a nonparametric Kruskal-Wallis was used to test for significant differences in floral sex ratios between umbel orders. It was also used to analyze mean seed set among pollination treatments and umbel orders within open pollinated plants in the breeding system experiment. We used Pearson's chi-square test (proportions parameters test) to analyze differences in percent germination among pollination treatments.

Results

Floral phenology and sex expression

The mean duration of the flowering sequence for an umbel in *Ptilimnium nodosum* is 9.48 days (±1.27) and the proportion of perfect flowers in each stage is reported in Table 3.2. Because dichogamy occurs within perfect flowers and within and among sequentially blooming umbel orders, flowers are never all in the same stage at once. The separation in phases within a flower was absolute and anthers had fully dehisced before stigmas became receptive. In contrast, asynchronous flowering within an umbel resulted in frequent overlap between male and female stages, which typically lasted 1-2 d each. Umbels were predominantly male for the first half of the flowering sequence yet, interfloral protandry appears to be weakly developed in *P. nodosum*. Continuous interfloral phenological observations of several flowers showed that many anthers begin dehiscing within 15 min of flower opening and continue beyond the onset of stigma receptivity. On days 7-9, the number of spreading stigmas increases from 18% to 78%. During this time period, the number of plants shedding pollen systematically decreases from 27% to 5%. Therefore, the phenotypic sex ratio and opportunity to sire seeds increase in favor of the female-phase flowers where the ovule to pollen ratio is greatest.

Approximately 90% of all umbels observed demonstrated overlap between sexual phases. The proportion of flowers in the female phase synchronous with flowers in the male phase was highly variable, ranging from 1% to 97% (n = 87 umbels) and typically occurred on day 8 of the flowering sequence. In an attempt to identify patterns in this variation, we divided these proportions into two groups: 0-50% (low synchrony) and 51-100% (high synchrony) and calculated the male to female ratio for each group (Table 3.3). These results indicate that when overlap between sexual phases was low (0-50%) the male to female ratio was high and, conversely, when overlap is high (51-100%) the male to female ratio is low. Both patterns suggest a mechanism for regulating self-fertilization by temporally limiting the availability of male and female gametes.

The opportunity for geitonogamy among sequentially blooming umbels (within a single flowering stalk) decreased with higher umbel orders and was greatest between primary and secondary orders where 50% (n = 28) of flowers were receptive simultaneously with anther dehiscence (Fig. 3.1). Overlap in sexual phases occurred 33% (n = 27) of the time between secondary and tertiary umbels and 0% (n = 15) between tertiary and quaternary order umbels, principally because flowers in quaternary umbels didn't open until several days and even weeks after flowers in tertiary umbels were already spent. These data suggest that the strength of interfloral dichogamy increases with umbel order, thus the opportunity for selfing decreases. On average, phases overlapped by <1 d between primary and secondary umbels (0.760 d) as well as between secondary and tertiary umbels (0.667 d).

Likewise, 59% of 100 plants sampled had more than one flowering stalk, indicating multiple opportunities for geitonogamy within an individual. The mean proportion of staminate flowers increased with umbel order, but was greatest and highly significant in tertiary umbels (Fig. 3.2; $F = 6.260$, $P<0.001$). Surprisingly, quaternary umbels had only 3% more staminate flowers than primary umbels despite a large decrease in total flower number. On average, there are 74 ± 12 flowers per primary umbel and 15 ± 7 flowers per quaternary umbel. These results are contrary to those reported for other protandrous, apioid umbellifers where quaternary umbels are often completely staminate. Although there is variation in sex expression among sequentially blooming umbel orders, other studies have found floral sex ratios, even between species, to be relatively constant (Bell, 1971; Cruden, 1976; Lloyd, 1979; Lovett-Doust, 1980).

Mating systems

Because results from all nonparametric tests agreed with one-way ANOVA, only parametric data are reported. A post-hoc Tukey's HSD test was conducted to determine which combinations of treatments and umbel orders were significantly different from one another in mean seed set.

On average, stigma receptivity as determined by the peroxidase test occurs on day 4 ($n = 20$) of the flowering sequence and typically lasts 2 d. These results corroborate visual estimations of receptivity when elongated styles are spreading and stigmatic surfaces appear sticky or wet. Differences in mean seed set among pollination treatments were statistically significant (Fig. 3.3; F = 15.500; P<0.001). Seed set was particularly low in both the autogamy and manual selfing treatments (1.2 and 1.0%, respectively), in spite of the high incidence of overlap between sexual phases within an umbel. Seed sets of geitonogamy, open-pollinated (control), and manually outcrossing flowers (21, 25, and 26%), however did not significantly differ from one another, suggesting that control flowers were pollinated by both self and outcross pollen. These data indicate that while *Ptilimnium nodosum* is self-compatible, insect-mediated pollination is critical to sexual reproduction. Given its sequential flowering sequence and low autogamous seed set, geitonogamy accounts for a substantial proportion of self-fertilization. This is evidenced by weak interfloral protandry and the production of multiple flowering stalks per plant, which increases the opportunity for geitonogamy.

Mean seed set among umbel orders was significantly different than expected by chance alone for openly pollinated plants (Fig. 4; F = 9.959, P<0.01), consistently decreasing with umbel order. Seed set was highest among primary umbels (40%, respectively) and closely tracked the proportion of perfect flowers in sequentially blooming umbel orders (Fig. 3.2). As the number of perfect flowers decreased (and staminate flowers increased) with umbel order so did the number of flowers to set seed. While seed set for quaternary umbels was omitted from analysis, the data show that only 19% of all plants sampled produced quaternary umbels and only 25% (1/4) of these umbels actually set seed, which was particularly low (~3%).

Germination rate

Germination differed significantly among seeds produced by different pollination treatments (Pearson $\chi^2 = 8.645$, $P<0.05$), but was highest in the manual selfing treatment (74%). A 64% germination rate was observed for manual outcrossing, followed by 54% for geitonogamy and 47% for openly pollinated plants.

Discussion

Consequences of floral attributes

The results of this study show that *P. nodosum* has a mixed mating system highly dependent on insect-mediated pollination. Experimental cross-pollination treatments demonstrate that the species readily outcrosses, although the combination of weak interfloral protandry and vegetative reproduction allows multiple opportunities for geitonogamy at a rate comparable to outcrossing. These data also suggest that inbreeding doesn't appear to negatively affect seed production or germination rate, which is expected given the species' mixed mating system. The absence of autogamy observed in *P. nodosum* (mean seed set for natural and manual autogamy combined = ~1%) is partly due to strong intrafloral protandry. Within a flower, anthers dehisce sequentially before stigmas become receptive. Separation in sexual phases between flowers of the same umbel, however, is not complete but low male to female ratios precludes autogamy. Because selfing occurs mostly through geitonogamy, it has probably not been directly selected for per say, but it a side-effect of the selection for protandry (*sensu* Eckert, 2000).

Bell (1971) suggests that differences in the strength of protandry can produce different pollination patterns as a result of variation in sexual expression, particularly the increased proportion of staminate flowers in higher umbel orders. He argued that because stigmas aren't receptive until after anthers have dehisced in plants with repeated cycles of protandry, the last order of umbels to bloom will likely remain unpollinated. Given that perfect flowers are initially male, female-phase flowers will open into an environment where pollen is readily available (Aizen, 1997; Sargent and Roitberg, 2000). Consequently, the concentration of perfect flowers in earlier-blooming umbels that could be pollinated by staminate flowers from later blooming umbel orders would be selected for. A corollary to this hypothesis is that the clustering of perfect flowers by individual plants closely follows pollinator abundance and activity (Schlessman, 1982; Thompson, 1989).

This phenotypic pattern is largely represented in *P. nodosum* as seed set in open pollinated plants decreased with higher umbel orders. This is partly due to the decreasing proportion of perfect flowers, but may also be a consequence of seasonal changes in mating opportunities due to pollen limitation or less resource availability due to seed maturation in earlier flowering umbels. Marked protandry is expected to produce a seasonal shift in phenotypic sex ratios from a predominantly female to highly male flower population (Wells and Lloyd, 1991; Brunet and Charlesworth, 1995; Konuma and Yahara, 1997; Sargent and Roitberg, 2000). Aizen (2001) investigated the effects of seasonal variation in flower sex ratio and pollinator abundance on the pollination dynamics in the protandrous plant, *Alstroemeria aurea* and found that pollination was highly influenced by the seasonal decrease in the abundance of male-phase flowers. Aizen recorded decreased levels of pollen carried by pollinators and thus the amount of pollen deposited per insect visit was also reduced. At the end of the flowering season, the small proportion of male-phase flowers translates into decreased pollen receipt for female-phase flowers. Although absolute protandry in *P. nodosum* is incomplete, it is possible that pollination is insufficient in the highest umbel orders and may be attributed to low floral density or lack of pollinators and successful pollen deposits late in the flowering season. This could be one explanation for the low seed set observed in quaternary umbels despite the relatively high proportions of perfect flowers.

Implications for conservation

The majority of apioid taxa exhibit mixed mating systems (Koul et al., 1993). Yet, while *P. nodosum*'s breeding system is adapted to outcrossing and seed set is moderate, the opportunity to establish new sites downstream via seed dispersal is spatially and temporally dynamic (Maddox, 1991; USFWS, 1990). Seeds lack structures to facilitate long-distance dispersal and often germinate directly beneath the parent plant (USFWS, 1990), although the ability of the species to seed bank is unknown. Seeds readily float and dispersal is facilitated by water flow, but Maddox and Bartgis (unpub. data) report significant rates of winter flooding mortality among seedlings in Sideling Hill Creek. In addition, suitable habitat is scarce and alterations in hydrological dynamics due to impoundments and sedimentation caused by land use change chronically threaten the species (USFWS, 1990). Furthermore, because *P. nodosum* occupies a narrow range of water depths, fluctuations and variability in water levels suggests establishment is an uncommon event. All of these factors indicate that seed dispersal to new sites is probably limited, but the species' small stature and spotty distribution make the discovery of new populations extremely difficult.

The opportunity to self, in combination with vegetative reproduction, however, may be of great importance to the short-term persistence of the species and increase the likelihood of colonizing new locations. As previously stated, vegetative shoots are produced at the nodes of decumbent flowering stems and develop into individual plantlets following winter dieback. Extensive root production may help to secure the new plantlet to a substrate that is frequently eroded by heavy water flow and facilitate resource uptake (USFWS, 1990). Self-fertilization also ensures reproduction when mates are limited due to founding events. The importance of reproductive assurance, however, is controversial since most experimental studies (including this one) have demonstrated that geitonogamous and outcross pollen do not limit seed production and autogamous self-fertilization provides no contingency plan (Leclerc-Potvin and Ritland, 1994; Klips and Snow, 1997; Eckert and Schafer, 1998; but see Anderson et al., 2003). In *P. nodosum*, autogamous selfing is almost non-existent and if flowers are not outcross-pollinated (i.e. due to low pollinator activity) and incapable of autogamous selfing, reproductive output will be severely reduced (Elle and Hare, 2002).

The interaction between contrasting reproductive strategies (sexual vs. asexual) may be a consequence of a patchy environment (Pandit and Babu, 2003). Because sexual recruitment is limited in *P. nodosum* and other clonal species (Eckert and Barrett, 1993), vegetative propagation may have evolved for several reasons. Unlike autogamous selfing, asexuality provides reproductive assurance when sexual modes are unsuccessful in the aquatic environment. Since most selfing occurs through geitonogamy, pollen and seed discounting may be severe. Low plant density can result in a shift from outcrossing to selfing (Jain, 1976; Barrett and Kohn, 1991; Van Treuren et al., 1993) and reproductive assurance may therefore only be guaranteed through clonal spread and the benefits of vegetative reproduction may outweigh the fitness costs of geitonogamy. If sufficiently effective, vegetative reproduction may reduce the selective value of sexual reproduction (Grace, 1993). Furthermore, asexuality favors high immediate fitness by facilitating resource acquisition and spreading the risk of genet death among several independent ramets (Cook, 1979; Kral, 1981; Handel, 1985; Grace, 1993; Hutchings and Wijesinghe, 1997; Holsinger, 2000). While vegetative reproduction in *P. nodosum* provides immediate fitness advantages, there are drawbacks to clonality in rare and endangered species, including the difficulty in calculating census population sizes because genets may be impossible to differentiate from vegetative ramets and thus the genetic structure of a population may be incorrectly estimated. In many species, asexual reproduction is facultative and often mixed with some facility for sexual reproduction (Stebbins, 1957) and several authors have reported on the retention of sexual reproduction by clonal species (Ellstrand and Roose, 1987; Eriksson, 1992, 1993; Pandit and Babu, 2003) and its role in the maintenance of genetic variation for long-term adaptability to changing environmental conditions. In *P. nodosum*, low levels of genetic diversity, however, in combination with reduced seed production, seedling recruitment, and an increase in population size via clonal growth alone may increase the species' risk of extinction.

Conclusions

In light of *P. nodosum*'s moderate seed production and germinability, it seems that environmental conditions, not mating system attributes, are limiting factors to the species' distribution and abundance. A habitat specialist, microsite characteristics are probably critical to the species' persistence and hydrological events create the conditions necessary for survival. As previously mentioned, stream channel scouring eliminates competition for *P. nodosum*, but may also play a key role in transporting fine sediment to interstitial spaces between gravel and exposed bedrock, a habitat predominately utilized by the species. In addition, the timing of flow events is often tied to the life history strategies and phenologies of many riparian plants, from the seasonal sequence of flowering to seed dispersal, establishment and growth (Rea and Ganf, 1994; Poff et al., 1997; Bunn and Arthington, 2002; Poff and Lytle, 2004). Therefore, the considerable seedling mortality rates observed by Maddox and Bartgis (unpub. data) in a Maryland population of *P. nodosum* may be due to an altered flow regime. That is, changes in the frequency, magnitude, or predictability of flow events could result in the break up of adaptations synchronized with long-term hydrological dynamics (Poff and Lytle, 2004). An early flood, for example, could damage or eliminate seedlings before they are sufficiently established. If the species is highly adapted to specific flow characteristics, then it might be vulnerable to flow regime alteration and small *P. nodosum* populations, like the one in North Carolina, are at risk of being extirpated by stochastic events. Therefore, the identification of hydrological parameters most critical to *P. nodosum* survival is recommended.

As we considered only one small ex situ population in this garden study, it is important to note that the results demonstrated here do not necessarily reflect the breeding patterns among all ecotypes. Trends in *P. nodosum*'s reproductive biology, therefore, need to be confirmed across its entire range. Studies have demonstrated that floral traits and reproductive mode can differ among populations within a species (Ellstrand and Roose, 1987; Eckert and Barrett, 1993; Xie et al., 2001; Elle and Hare, 2002; Gross and Caddy, 2006), which may be particularly true for *P. nodosum* ecotypes. Plant breeding systems depend on many abiotic and biotic factors that can affect pollination and vary widely among populations. Likewise, it is difficult to infer potential adaptations of species to natural flow regimes if hydrological conditions across the species' range are unknown. Nonetheless, this study does shed light onto the basic biology of *P. nodosum* as well as the role of floral features in regulating the species' breeding system. Above all, this study represents an important step in understanding reproductive strategies utilized by *P. nodosum* and, in conjunction with knowledge of site-specific environmental conditions, can inform conservation managers on how to best protect the species.

Figures

Figure 3.1 Opportunities for geitonogamy within a flowering stalk. In order for geitonogamy to occur, at least one flower must be in anthesis during the same period that stigmas from one or more flowers of an earlier blooming umbel order are receptive. Synchrony in sexual phases was calculated by dividing the number of times sexual phases between umbel orders overlapped divided by the total number of umbels sampled in the preceding order.

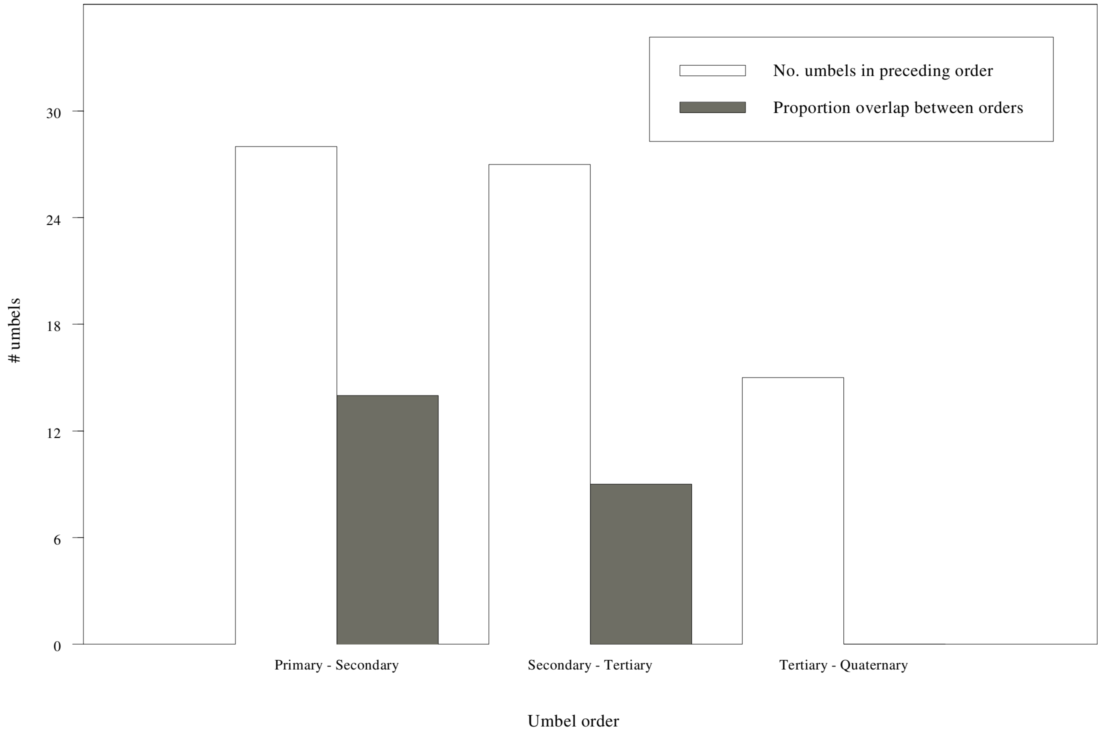


Figure 3.2 Variation in sex expression among sequentially blooming umbel orders. Vertical bars represent 1 SD and different letters indicate significantly different values in the mean proportion of staminate flowers (ANOVA, P<0.001).

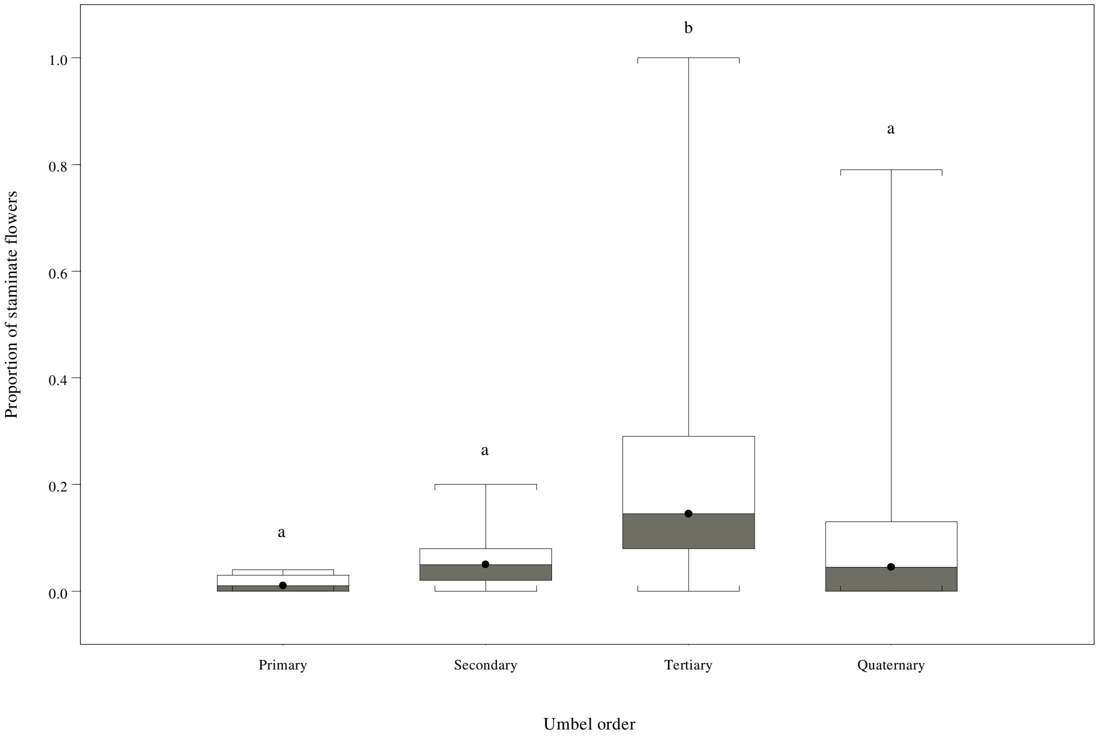


Figure 3.3 Mean seed set among different pollination treatments performed in 2006. Error bars represent 1 SD and different letters indicate significantly different values (ANOVA, P<0.001).

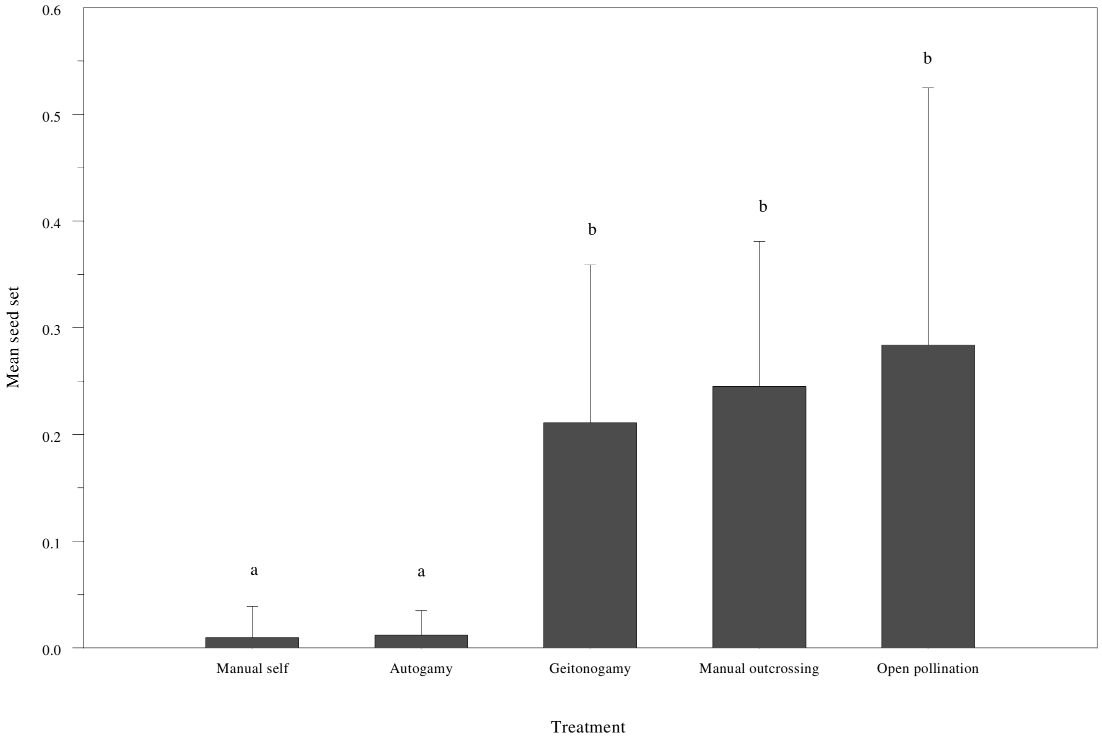
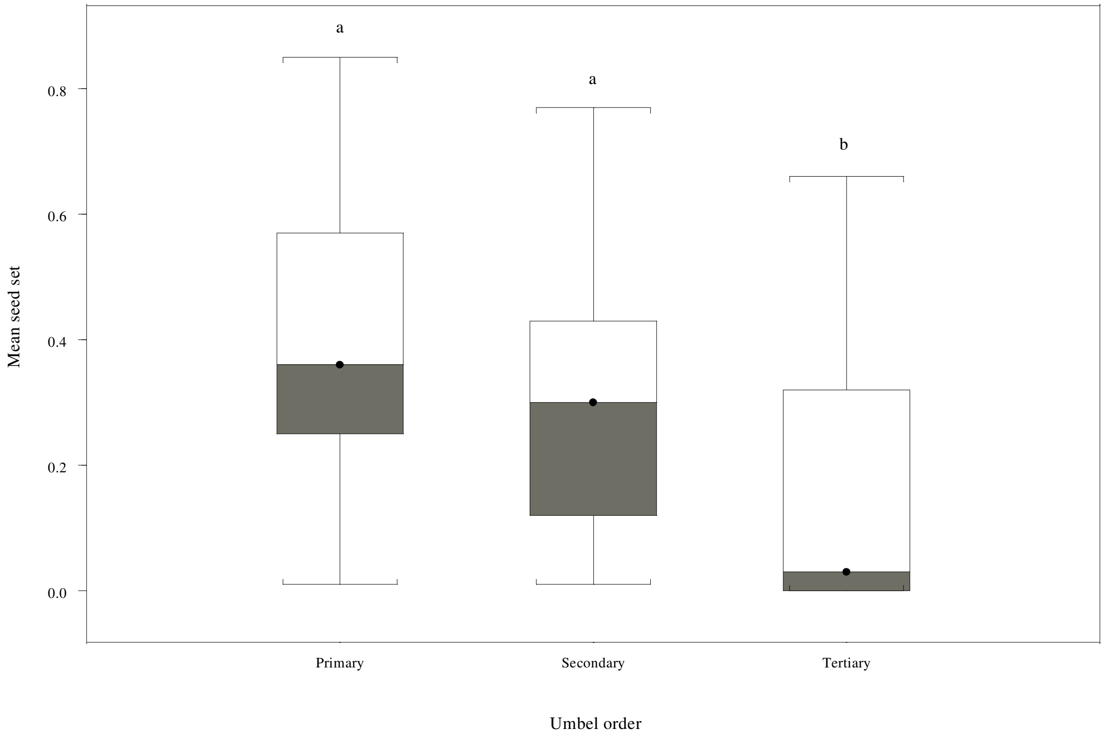


Figure 3.4 Variation in mean seed set among sequentially blooming umbel orders in open-pollinated individuals. Quaternary umbels were excluded from analysis because too few were produced for statistical analysis; < 20% of all individuals produce forth order umbels. Vertical bars represent 1 SD and different letters indicate significantly different values (ANOVA, P<0.01).



Tables

Table 3.1 Pollination treatments performed in breeding system study of *Ptilimnium nodosum*. Eighteen individuals were randomly selected for each treatment (22 for control), which was integrated across an entire umbel. The number of flowers pollinated per treatment was approximately equal.

Treatment	Description	# flowers
Open pollination	Unmanipulated (control)	967
Manual outcrossing	Caged, occluded and pollinated with pollen from a different plant	1119
Autogamy	Caged only	1136
Manual selfing	Caged and manually pollinated within a flower	1107
Geitonogamy	Caged, occluded and manually pollinated with pollen from the same flowering stalk	1023

Table 3.2 Stage-based floral phenology for *Ptilimnium nodosum*. The relative proportion of perfect flowers in each state per day was calculated and averaged across all umbel orders. The mean duration of the flowering sequence in a typical *P. nodosum* umbel = 9.48 days (±1.27) and *n* = number of umbels sampled on each day. A total of 28 primary, 30 secondary, 24 tertiary, and 15 quaternary umbel orders from 30 individuals were scored.

	Day									
Stage	1	2	3	4	5	6	7	8	9	10
1	0.898	0.758	0.570	0.377	0.196	0.068	0.017	0.001	0.000	0.000
2	0.064	0.104	0.141	0.152	0.147	0.106	0.045	0.009	0.000	0.000
3	0.037	0.137	0.234	0.317	0.353	0.353	0.268	0.135	0.044	0.007
4	0.000	0.000	0.056	0.153	0.302	0.449	0.492	0.352	0.174	0.144
5	0.000	0.000	0.000	0.000	0.002	0.025	0.182	0.506	0.783	0.849
n	97	97	97	97	97	97	97	92	78	46

Table 3.3 Relative synchrony in male and female sexual phases. The mean proportion of flowers in the female phase open simultaneously with flowers in the male phase on the same plant and therefore capable of geitonogamous pollination is reported. Although overlap occurred ~50% of the time, data were highly variable and thus divided into two groups representing low (0-50%) and high (51-100%) synchrony. The ratio of male to female flowers was calculated to estimate the contribution of each sex to potential geitonogamous pollinations.

Group	***n***	**Proportion in synchrony**	**Male : female**
0-50%	41	0.231 ± 0.153	1.391 ± 1.351
51-100%	46	0.735 ± 0.139	0.151 ± 0.128

Notes: Values ranged from zero to 1.0, where zero corresponds to complete separation in sexual phases and 1.0 to the simultaneous expression of both phases (also see Dudash and Fenster, 2001). Data reported are mean ± 1 SD and represent the strength of interfloral dichogamy in *Ptilimnium nodosum*. Number of umbels = *n*.

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IV. CONCLUSIONS, SYNTHESIS, AND FUTURE DIRECTIONS

The task of protecting biological diversity is challenging and requires that attention be paid to all hierarchical levels of biological organization from genes and species to ecosystems and landscapes (Noss and Cooperrider, 1994). Biodiversity also encompasses the processes, both ecological and evolutionary, that create and maintain the full array of life; successful conservation must therefore incorporate a variety of strategies. The work presented in this thesis begins with a broad scale examination of plant rarity within habitats, ecosystems, and landscapes of the Southeastern U.S. The focus on a single rare species and some of the processes that control genetic structure, population dynamics, and distribution are critical to species-based conservation and provide an important addendum to broader, conservation planning efforts. Combined, this work achieves a more holistic approach to rare plant conservation in the Southeast.

First, few studies have explored large-scale patterns of rarity with respect to multiple factors, particularly in the Southeast. Biogeographic analyses of plant endemism (Estill and Cruzan, 2001; Loehle, 2006) and species endangerment (Dobson et al., 1997; Flather et al., 1998) in the Southeastern U.S. have highlighted the significance of regionally important floras and biodiversity hotspots, but frequently fall short of identifying ecological correlates responsible for such patterns. My work expands on previous studies by targeting globally imperiled rare species and provides a more complete picture of rarity among vascular plants by combining geographical, ecological, and taxonomic drivers of rarity. Second, the focus here on ecoregions as a geographic unit of analysis provides a meaningful, ecologically based framework for setting conservation targets at broad scales (Ricketts et al., 1999b) and reflects current approaches to conservation planning increasingly embraced by conservation organizations. The premise of broad scale conservation is that the greatest biodiversity, including rare species, will be conserved if the greatest diversity of habitats is represented in networks of protected areas (Olson and Dinerstein, 1998).

In addition, this work represents a first attempt to quantitatively determine the distribution and representation of rare plants with respect to habitat types and taxonomy in the Southeast. Others have examined the occurrence of rare plants in particular habitats (e.g. high elevation rock outcrops, cedar glades and prairies), but few have synthesized patterns across multiple habitats at broader scales. Using a habitat classification scheme developed for the flora of the Carolinas, I show the distribution of rare plants across 29 unique habitat types and identify those habitats with significantly more rare species than predicted by linear relationships.

Similarly, recent studies on the incidence of rarity as a function of taxonomic group size have shed light onto the predictability of extinction risk, but have primarily assessed patterns at continental or national scales (but see Domínquez Lozano and Schwartz, 2005). Furthermore, rates of rarity are not consistent across regions or floras (Edwards and Westoby, 2000), nor are the definitions for what constitutes a rare species. Several results described in this thesis for the Southeast, however, were consistent with other studies. Rare plants are consistently clustered within large plant families and the under-representation of rare plants in large plant families like Cyperaceae and Poaceae and the over-representation in Brassicaceae are also reported in Edwards (1998) for the Australian flora and in Edwards and

Westoby (2000) for North America. In contrast, smaller families like Isoetaceae had unexpectedly high numbers of rare plants not reported elsewhere, which may reflect a unique evolutionary history and center of diversity in the Southeast.

Finally, I take a case-study approach to examine the ecological and evolutionary processes in the rarity and persistence of a federally endangered plant, *Ptilimnium nodosum*. Very little is known about *P. nodosum* and my work on the reproductive biology of the species is an important contribution to recovery efforts. Understanding plant reproduction can guide transplantation, reintroduction, and ex situ conservation. In North Carolina, for example, propagation of the species allowed for its successful reintroduction to a historical location along the Deep River in 2006. Seeds from experimental cross pollinations are also stored at the North Carolina Botanical Garden as part of the Center for Plant Conservation's national ex situ conservation program. Plant material continues to be an important resource for research projects and land managers working with the species. Future research plans for *P. nodosum* include a hydrological study to determine the effects of an altered flow regime on species growth and survival. Specifically, this study will test different levels of flooding duration and turbidity on mean dry weight and reproductive output.

Challenges and remaining questions

While this research helps bridge the gap between pattern and process in rare plant conservation, many challenges and unanswered questions remain. First, regions rich in rare plant diversity do not frequently correspond to other taxonomic groups and the search for indicator taxa, or relatively well-known groups of organisms whose distributions can be used as a surrogate measure for the distribution patterns of other taxa, have produced mixed results (Prendergast et al., 1993; Jaarsveld et al., 1998, Ricketts et al., 1999b). Moreover, identifying general rules for explaining rarity based on particular plant traits, such as taxonomy, has generated little consensus. My work does not attempt to reconcile the differences in the rates of rarity between studies or the definition of rarity, which has been the subject of much debate in the literature. Species attributes are more likely to be a consequence of their particular geographic and ecological setting where speciation and persistence has occurred (Gaston, 1994). This work does, however, provide a necessary step for additional studies concerning biogeographical and evolutionary drivers of taxonomic patterns unique to the Southeast.

Clearly, there is not enough time or resources available to examine every rare species with pressing conservation needs in full, exhaustive detail. Understanding individual species biology and management requirements is essential to long-term conservation success, but managers will have to balance the needs of individual species with broader, landscape level conservation objectives.

Although my work on *Ptilimnium nodosum* has answered several important research questions, there is much to be learned about the species, particularly its biological interactions with associated species. For example, *P. nodosum* is frequently found among thick mats of *Justicia americana*, a common, clonal plant capable of vegetative reproduction and adapted to natural flow fluctuations because of a deeply rooted, rhizomatous growth form. Studies have reported on the role of *J. americana* in habitat modification (Fritz and Feminella, 2003) and streambed stabilization (Fritz et al., 2004), yet its interaction with *P. nodosum* is unknown and raises several important research questions.

First, what (if any) are the competitive effects of a close association between the two species? Second, by reducing water current velocity and increasing fine sediment deposition, does *J. americana* facilitate *P. nodosum* establishment and survival? Or, do the low light levels and increased turbidity associated with macrophyte beds create suboptimal conditions for *P. nodosum*? The two species share many traits, suggesting that *P. nodosum* may facilitate its own establishment and survival. Although rarely in large abundance throughout its range, *P. nodosum*, like *J. americana*, often forms thick, vegetative mats. It's possible that *P. nodosum* also provides a stable, protected substrate for the germination of seeds or rooting of vegetative offshoots.

While I discuss the significance of clonality and vegetative reproduction in *P. nodosum*, the clonal structure of the species in unknown and offers many opportunities for further research. Cook (1983) argues that knowledge of genet spatial configuration can inform studies of competition, gene flow, and demography in clonal plant populations. The occupation of horizontal space, for example, may be affected by features of the habitat that cause the position of ramets to be highly variable. In a patchy environment such as riverside scour glades, the capacity to detect differences in resource levels, and develop adventitious roots and shoots may significantly increase the success of *P. nodosum* clones (Cook, 1983). Clonal spread may also be critical to the rapid colonization of sites in highly disturbed habitats (Fahrig et al., 1994). Although identifying individual genets in *P. nodosum* and other clonal species is difficult since vegetative branching often occurs below ground, knowledge of clonal structure in combination with site-specific environmental conditions can enhance our understanding of *P. nodosum* persistence.

Appendices

Appendix I. Rare Southeastern vascular plants sorted by plant families. Botanical nomenclature follows Weakley (2006).

Family	Botanical Name	Range
Acanthaceae	*Ruellia noctiflora*	AL, FL, GA, MS
Adoxaceae	*Viburnum bracteatum*	AL, GA, TN
Alisamataceae	*Echinodorus floridanus*	FL
Alisamataceae	*Sagittaria fasiculata*	GA, NC, SC
Alisamataceae	*Sagittaria secundifolia*	AL, GA
Alliaceae	*Allium oxyphilum*	WV
Alliaceae	*Allium speculae*	AL, GA
Amaranthaceae	*Amaranthus pumilus*	DE, MD, NC, SC, VA
Amaryllidaceae	*Hymenocallis choctawensis*	AL, FL, GA, MS
Amaryllidaceae	*Zephyranthes simpsonii*	FL, GA, NC, SC
Anacardiaceae	*Rhus michauxii*	GA, NC, VA
Apiaceae	*Angelica dentata*	FL, GA
Apiaceae	*Oxypolis canbyi*	GA, NC, MD, SC
Apiaceae	*Ptilimnium ahlesii*	GA, NC, SC
Apiaceae	*Ptilimnium nodosum*	AL, GA, MD, NC, SC, VA, WV
Apiaceae	*Thaspium pinnatifidum*	AL, GA, KY, NC, TN
Apocynaceae	*Asclepias viridula*	AL, FL, GA
Apocynaceae	*Matelea alabamensis*	AL, FL, GA
Aquifoliaceae	*Ilex cuthbertii*	GA, SC
Aristolochiaceae	*Hexastylis rhombiformis*	NC
Aristolochiaceae	*Hexastylis speciosa*	AL
Asteraceae	*Arnoglossum album*	FL
Asteraceae	*Arnoglossum diversifolium*	AL, FL, GA
Asteraceae	*Balduina atropurpurea*	AL, FL, GA, NC, SC
Asteraceae	*Boltonia apalachicolensis*	FL, MS
Asteraceae	*Brickellia cordifolia*	AL, FL, GA
Asteraceae	*Chrysopsis godfreyi*	AL, FL
Asteraceae	*Cirsium lecontei*	AL, FL, GA, MS, NC, SC
Asteraceae	*Coreopsis integrifolia*	FL, GA, SC
Asteraceae	*Coreopsis pulchra*	AL, GA
Asteraceae	*Echinacea laevigata*	GA, NC, SC, VA
Asteraceae	*Echinacea tennesseensis*	TN
Asteraceae	*Eupatorium anomalum*	AL, FL, GA, SC,
Asteraceae	*Eurybia saxicastellii*	KY, TN

Family	**Botanical Name**	**Range**
Asteraceae	*Eurybia spinulosa*	FL
Asteraceae	*Hartwrightia floridana*	FL, GA
Asteraceae	*Helianthus smithii*	AL, GA, TN
Asteraceae	*Helianthus verticillatus*	AL, GA, TN
Asteraceae	*Liatris helleri*	NC, VA, WV
Asteraceae	*Liatris oligocephala*	AL
Asteraceae	*Marshallia grandiflora*	KY, MD, NC, TN, WV
Asteraceae	*Marshallia ramosa*	FL, GA
Asteraceae	*Packera millefolium*	GA, NC, SC, VA
Asteraceae	*Pityopsis ruthii*	TN
Asteraceae	*Rudbeckia auriculata*	AL, FL, GA
Asteraceae	*Rudbeckia heliopsidis*	AL, GA, NC, SC, VA
Asteraceae	*Silphium brachiatum*	AL, TN
Asteraceae	*Silphium glutinosum*	AL
Asteraceae	*Silphium perplexum*	AL
Asteraceae	*Solidago albopilosa*	KY
Asteraceae	*Solidago plumosa*	NC
Asteraceae	*Solidago shortii*	KY
Asteraceae	*Solidago simulans*	GA, NC, SC
Asteraceae	*Solidago spithamaea*	NC, TN
Asteraceae	*Solidago villosicarpa*	NC
Asteraceae	*Symphyotrichum chapmanii*	AL, FL
Asteraceae	*Symphyotrichum depauperatum*	MD, NC
Asteraceae	*Symphyotrichum georgianum*	AL, FL, GA, NC, SC
Asteraceae	*Symphyotrichum rhiannon*	NC
Asteraceae	*Verbesina heterophylla*	FL
Boraginaceae	*Onosmodium decipiens*	AL
Brassicaceae	*Arabis georgiana*	AL, GA
Brassicaceae	*Boechera laevigata*	VA, WV
Brassicaceae	*Boechera perstellata*	KY, TN
Brassicaceae	*Cardamine micranthera*	NC, VA
Brassicaceae	*Leavenworthia alabamica*	AL
Brassicaceae	*Leavenworthia crassa*	AL
Brassicaceae	*Paysonia lyrata*	AL
Brassicaceae	*Paysonia perforata*	TN
Brassicaceae	*Paysonia stonensis*	TN
Brassicaceae	*Physaria globosa*	KY, TN
Calycanthaceae	*Calycanthus brockianus*	GA
Campanulaceae	*Lobelia boykinii*	AL, FL, GA, MS, NC, SC

Family	**Botanical Name**	**Range**
Caryophyllaceae	*Minuartia cumberlandensis*	KY, TN
Caryophyllaceae	*Minuartia godfreyi*	AL, FL, GA, NC, TN, VA
Caryophyllaceae	*Paronchia rugelii*	FL, GA
Caryophyllaceae	*Silene polypetala*	GA
Celastraceae	*Paxistima canbyi*	KY, MD, TN, VA, WV
Cistaceae	*Hudsonia montana*	NC
Convoluvaceae	*Cuscuta harperi*	AL, GA
Cyperaceae	*Carex acidicola*	AL, GA
Cyperaceae	*Carex brysonii*	AL
Cyperaceae	*Carex impressinervia*	AL, MS, NC, SC
Cyperaceae	*Carex lutea*	NC
Cyperaceae	*Carex radfordii*	GA, NC, SC
Cyperaceae	*Carex roanensis*	GA, KY, NC, TN, VA, WV
Cyperaceae	*Carex thornei*	AL, FL, GA
Cyperaceae	*Carex timida*	AL, KY, TN
Cyperaceae	*Fimbristylis brevivaginata*	AL, GA, VA
Cyperaceae	*Fimbristylis perpusilla*	DE, GA, MD,NC, SC, TN
Cyperaceae	*Rhynchospora crinipes*	Al, FL, GA, MS, NC
Cyperaceae	*Rhynchospora culixa*	FL, GA
Cyperaceae	*Rhynchospora knieskernii*	DE
Cyperaceae	*Rhynchospora punctata*	FL, GA
Cyperaceae	*Rhynchospora solitaria*	GA
Cyperaceae	*Schoenoplectus hallii*	GA
Cyperaceae	*Scirpus flaccidifolius*	VA, NC
Diapensiaceae	*Shortia galacifolia var. brevistyla*	NC
Diapensiaceae	*Shortia galacifolia var. galacifolia*	GA, NC, SC
Ericaceae	*Elliotia racemosa*	GA, SC
Ericaceae	*Rhododendron eastmanii*	SC
Ericaceae	*Rhododendron chapmanii*	FL
Eriocaulaceae	*Eriocaulon koernickianum*	GA
Euphorbiaceae	*Croton elliottii*	AL, FL, GA, SC
Fabaceae	*Aeschynomene virginica*	MD, NC, VA
Fabaceae	*Apios priceana*	AL. KY, MS, TN
Fabaceae	*Astragalus bibullatus*	TN
Fabaceae	*Baptisia arachnifera*	GA
Fabaceae	*Baptisia megacarpa*	AL, FL, GA
Fabaceae	*Chamaecrista deeringiana*	FL, GA, MS
Fabaceae	*Dalea cahaba*	AL
Fabaceae	*Dalea foliosa*	AL, TN

Family	**Botanical Name**	**Range**
Fabaceae	*Desmodium ochroleucum*	AL, FL, GA, DC, DE, MD, MS, NC, TN, VA
Fabaceae	*Orbexilum virgatum*	FL, GA
Fabaceae	*Trifolium calcaricum*	VA, TN
Fagaceae	*Quercus boytonii*	AL
Gentianaceae	*Sabatia capitata*	AL, GA, NC, TN
Grossulariaceae	*Ribes echinellum*	FL, SC
Hydrophyllaceae	*Phacelia covillei*	DC, MD, NC, VA
Hymenopyllaceae	*Hymenophyllum tayloriae*	AL, GA, NC, SC, TN
Hypericaceae	*Hypericum exile*	FL
Hypericaceae	*Hypericum lissophloeus*	FL
Illiaceae	*Illicum parviflorum*	FL, GA
Iridaceae	*Calydorea coelestina*	FL
Iridaceae	*Sisyrinchium dichotomum*	NC, SC
Isoetaceae	*Isoetes boomii*	GA
Isoetaceae	*Isoetes georgiana*	GA
Isoetaceae	*Isoetes hyemalis*	AL, FL, GA, NC, SC, VA
Isoetaceae	*Isoetes junciformis*	GA
Isoetaceae	*Isoetes louisianensis*	AL, MS
Isoetaceae	*Isoetes melanospora*	GA, SC
Isoetaceae	*Isoetes microvela*	NC
Isoetaceae	*Isoetes tegetiformans*	GA
Isoetaceae	*Isoetes tennesseensis*	TN
Isoetaceae	*Isoetes virginica*	NC, VA
Juncaceae	*Juncus caesariensis*	MD, NC, VA
Lamiaceae	*Blephilia subnuda*	AL
Lamiaceae	*Conradina glabra*	AL, FL
Lamiaceae	*Dicerandra radfordiana*	GA
Lamiaceae	*Macbridea alba*	FL
Lamiaceae	*Macbridea caroliniana*	GA, NC, SC
Lamiaceae	*Pycnanthemum clinopodioides*	DE, MD, NC, VA, WV
Lamiaceae	*Pycnanthemum torreyi*	DE, KY, MD, NC, SC, TN, VA, WV
Lamiaceae	*Scutellaria alabamensis*	AL
Lamiaceae	*Scutellaria altamaha*	GA, NC, SC
Lamiaceae	*Scutellaria glabriuscula*	AL, FL, GA, MS
Lamiaceae	*Scutellaria ocmulgee*	GA
Lamiaceae	*Stachys clingmanii*	NC, SC, TN
Lauraceae	*Lindera melissifolia*	AL, GA, MS, NC, SC
Lauraceae	*Lindera subcoriacea*	AL, FL, GA, MS, NC, SC, VA
Lentibulariaceae	*Pinguicula ionantha*	FL

Family	**Botanical Name**	**Range**
Liliaceae	*Lilium iridollae*	AL, FL
Liliaceae	*Lilium pyrophilym*	NC, SC, VA
Loganiaceae	*Spigelia gentianoides var alabamensis*	AL
Loganiaceae	*Spigelia gentianoides var, gentianoides*	FL
Lythraceae	*Lythrum curtissii*	FL, GA
Magnoliaceae	*Magnolia ashei*	FL
Malvaceae	*Iliamna corei*	VA
Melastomataceae	*Rhexia parviflora*	FL, GA
Melastomataceae	*Rhexia salicifolia*	AL, FL
Najadaceae	*Najas filifolia*	FL, GA
Nartheciaceae	*Narthecium americanum*	SC
Oleaceae	*Forestiera godfreyi*	FL, GA, SC
Onagraceae	*Ludwigia brevipes*	GA, MD, NC, SC, VA
Onagraceae	*Ludwigia ravenii*	FL, NC, SC, VA
Onagraceae	*Ludwigia spathulata*	AL, FL, GA, SC
Onagraceae	*Oenothera riparia*	NC, SC
Orbanchaceae	*Agalinis acuta*	MD
Orbanchaceae	*Castilleja kraliana*	AL
Orbanchaceae	*Schwalbea americana*	FL, NC, SC
Orchidaceae	*Calopogon multiflorus*	AL, FL, GA, MS, NC, SC
Orchidaceae	*Corallorhiza bentleyi*	VA, WV
Orchidaceae	*Isotria medeoloides*	DE, GA, MD, NC, SC, TN, VA, WV
Orchidaceae	*Malaxis bayardii*	NC, VA, WV
Orchidaceae	*Platanthera chapmanii*	FL, GA
Orchidaceae	*Platanthera integrilabia*	AL, GA, KY, MS, SC, TN
Orchidaceae	*Pteroglossaspis ecristata*	AL, FL, GA, MS, NC, SC
Pinaceae	*Abies fraseri*	GA, NC, TN, VA, WV
Plantaginaceae	*Amphianthus pusillus*	AL, GA, SC
Plantaginaceae	*Penstemon dissectus*	GA
Poaceae	*Aristida mohrii*	AL, FL, GA, SC
Poaceae	*Calamagrostis cainii*	NC, TN
Poaceae	*Calamovilfa arcuata*	AL, TN
Poaceae	*Ctenium floridanum*	FL, GA
Poaceae	*Dichanthelium hirstii*	DE, GA, NC
Poaceae	*Eustachys floridana*	AL, FL, GA
Poaceae	*Glyceria nubigena*	NC, TN
Poaceae	*Sporobolus teretifolius*	GA, NC, SC
Polemoniaceae	*Phlox buckleyi*	VA, WV
Polemoniaceae	*Phlox pulchra*	AL

Family	**Botanical Name**	**Range**
Portulacaceae	*Portulaca biloba*	GA
Potamogetonaceae	*Potamogeton floridanus*	FL
Potamogetonaceae	*Potamogeton tennesseensis*	TN, VA, WV
Primulaceae	*Lysimachia fraseri*	AL, GA, NC, SC, TN
Primulaceae	*Lysimachia graminea*	AL
Ranunculaceae	*Clematis addisonii*	VA
Ranunculaceae	*Clematis morefieldii*	AL, TN
Ranunculaceae	*Clematis socialis*	AL, GA
Ranunculaceae	*Clematis viticaulis*	VA
Ranunculaceae	*Delphinium alabamicum*	AL
Ranunculaceae	*Heuchera alba*	VA, WV
Ranunculaceae	*Saxifraga caroliniana*	NC, TN, VA, WV
Ranunculaceae	*Thalictrum cooleyi*	FL, GA, NC
Ranunculaceae	*Thalictrum debile*	AL, GA, MS
Rosaceae	*Crataegus triflora*	AL, GA, MS
Rosaceae	*Crateagus harbisonii*	TN
Rosaceae	*Geum geniculatum*	NC, TN
Rosaceae	*Geum radiatum*	NC, TN
Rosaceae	*Neviusia alabamensis*	AL, FL, GA, TN
Rosaceae	*Spiraea virginia*	GA, KY, NC TN, VA, WV
Rosaceae	*Waldsteinia lobata*	GA, NC, SC
Salicaceae	*Salix floridana*	FL, GA
Santalaceae	*Buckleya distichophylla*	NC, TN, VA
Sapotaceae	*Sideroxylon alachuense*	FL, GA
Sapotaceae	*Sideroxylon thornei*	AL, GA, FL
Sarraceniaceae	*Sarracenia oreophila*	AL, GA, NC
Taxaceae	*Taxus floridana*	FL
Taxaceae	*Torreya taxifolia*	FL, GA
Tofieldiaceae	*Harperocallis flava*	FL
Trilliaceae	*Trillium discolor*	GA, NC, SC
Trilliaceae	*Trillium persistens*	GA, SC
Xyridaceae	*Xyris isoetifolia*	AL, FL
Xyridaceae	*Xyris longisepala*	AL, FL
Xyridaceae	*Xyris tennesseensis*	AL, GA, TN

Appendix II. Habitat classification descriptions and criteria after Weakley (2005).

Upland forested habitats

High elevation forests. This habitat includes spruce-fir and “northern hardwood” forests of the upper elevations of the Blue Ridge although some species in this category extend downward in elevation to red oak forests of ridges at 3500 feet and above.

Acid cove. This habitat is delimited by ravines and other “gathering” landforms with generally mesic soils that are highly acidic. Evergreen rhododendrons and other heaths are often prominent.

Rich cove. This habitat consists of nutrient-rich, mesic forests of moderately high to low elevations in the Blue Ridge and Blue Ridge escarpment. The forests are in “coves” or other “gathering” landforms, but can also be on open slopes or along small streams over the appropriate substrates.

Montane dry forest. This habitat consists of dry and dry-mesic oak, oak-pine, and pine-dominated forests of ridges and slopes at moderate to low elevations in the Blue Ridge, and with scattered occurrence in the upper Piedmont as well, especially on monadnocks and small mountain ranges disjunct from the Blue Ridge proper.

Lowland mesic forest. This habitat includes mesic slopes and flats along small streams in the Piedmont and upper Coastal Plain. Some of these species also extend into mesic (cove) habitats in the mountains.

Lowland acid dry forests. This habitat consists of dry and dry-mesic forests of the Piedmont and less often upper Coastal Plain, dominated by oaks and pines, and usually with an extensive and diverse shrub cover of heaths.

Lowland calcareous dry forest. This habitat consists of dry and dry-mesic forests over calcareous or mafic substrates. Many other taxa characteristic of these substrates occur primarily in open canopy settings and are therefore treated in the appropriate Woodland or Glade category.

Coastal Plain hammock. This habitat includes fire-protected mesic to xeric slopes and bluffs in the Coastal Plain, dominated by hardwoods and fire-intolerant species. Northwards into North Carolina, maritime forests are a main example of this type, but southwards it becomes more extensive and distinctive on protected slopes and bluffs.

Pine rocklands. Unique to the Miami Rock Ridge and other disjunct areas of South Florida, this habitat consists of fire-dependent open canopy forest of *Pinus elliotti* var. *densa* over a limestone substrate. A diverse array of tropical and subtropical plants endemic to South Florida characterize this habitat.

General upland forests. This category is used for species with broad ecological amplitudes that cut across multiple upland forest categories.

Bottomland and alluvial habitats

Coastal Plain blackwater bottomlands. This habitat includes of the floodplains and beds of large streams and rivers with headwaters in the Coastal Plain, flowing generally through acid, sandy, and/or humic substrates with dissolved organic matter exceeding suspended particulates. Components of this habitat range from temporally flooded natural levees to seasonally or nearly permanently flooded sloughs and backwaters, and also bog-like saturated conditions in some areas.

Brownwater bottomlands. This habitat is distributed across the Coastal Plain, Piedmont, and Mountains, consisting of floodplains and beds of large streams and rivers with headwaters in the Piedmont or Mountains with substantial loads of suspended particulates. Flooding regimes range from rarely flooded natural levees to seasonally or nearly permanently flooded sloughs and backwaters.

Coastal Plain calcareous wet flatwoods and bottoms. This habitat includes poorly drained wet flats in the outer Coastal Plain often associated (but not limited to) with small to medium streams and overlying calcareous substrate.

General bottomlands. This category is used for bottomland and alluvial taxa with little preference between the three habitats above.

Woodland and glade habitats

High elevation glades and woodlands. This habitat includes a variety of specialized high elevation, non-forested habitats, excluding summit cliffs. Notably, this includes grassy balds and graminoid-dominated rocky habitats with moderate slope.

Granite glades and woodlands. This habitat consists of outcrops, flat or sloping, over granite rocks, and associated glades and woodlands.

Mafic glades, woodlands, and prairies. This habitat consists of glades, barrens, and so-called "Piedmont prairies" associated with mafic and ultramafic rocks, in both the Piedmont and Mountains. In the Piedmont, the weathering of mafic rocks tends to create a flatter landscape with shrink-swell clays, promoting greater fire frequency and limiting root depth and growth rates of woody vegetation than in the regionally dominant felsic rock landscapes.

Calcareous glades, woodlands, and prairies. This habitat includes glades, barrens, prairies, and woodlands over limestone dolostone, and other calcareous rocks. This habitat best represented in the Ridge and Valley Province and even more so in the Interior Low Plateau.

Shale glades, woodlands, and prairies. This habitat is best represented in the extensive shale barrens of western Virginia, eastern West Virginia, western Maryland and southcentral Pennsylvania, with a few extending into eastern Kentucky, eastern Tennessee, northwestern Georgia, and northern Alabama.

Riverside scour glades. This habitat consists of prairie-like vegetation, characterized by generalized glade/woodland/prairie taxa. The open condition is maintained by periodic severe flooding which scours and batters away soil and woody vegetation. This community is better developed and hosts a greater number of tightly associated taxa in areas to the north and west, notably the Potomac River near Washington, D.C., various rivers of the Cumberland Plateau in Kentucky, Tennessee, and Alabama.

Dry pinelands (sandhills). This habitat includes Coastal Plain sandhills, sand scrub, and loamy upland sites associated with *Pinus palustris* and usually also with various oaks such as *Quercus laevis*, *Quercus incana*, *Quercus margaretta*, *Quercus geminata*, *Quercus marilandica* var. *marilandica*, and *Quercus stellata*.

Wet pinelands (savannas and flatwoods). This habitat includes wetlands and moist uplands dominated by *Pinus palustris* (sometimes mixed with *Pinus serotina*, *Pinus elliottii* var. *elliottii*, and *Taxodium ascendens*, and generally with a complete absence of *Quercus* spp. This includes narrow, ecotonal areas between dry pinelands and streamhead pocosins in sandhill landscapes.

General woodlands and glades. This category is used for sun-loving taxa that are very generally distributed in woodlands, glades, and prairies (or at least cross-cutting many of the habitats under this category). Many of these taxa are now usually seen by the casual observer on roadbanks and under powerline rights-of-way.

Saturated boggy habitats

Coastal Plain natural ponds and depression meadows. This habitat includes natural depressional wetlands of the Coastal Plain, usually occurring in the context of a *Pinus palustris* matrix.

Coastal Plain pocosins. This habitat consists of acid wetlands in the Coastal Plain, in seepage-fed and ombrotrophic (blanket bog) situations, characteristically dominated by *Pinus serotina* and evergreen shrubs.

Montane fens, seeps, depressions, and wet meadows. This habitat consists of a variety of montane wetlands, mostly seepage-fed, over a range of substrates.

General wet acidic situations. This category is used for species of boggy habitats that are more generally distributed across these habitats.

Rock outcrop habitats

High elevation summit outcrops. This habitat consists of a very limited acreage on the higher summits of the Mountains, characterized by a very unique flora consisting of both narrow endemics and long-distance disjuncts from alpine boreal habitats further north.

Acid outcrops. This habitat consists of shaded and generally steep to vertical outcrops of acidic rocks.

Calcareous outcrops. This habitat consists of shaded and generally steep to vertical outcrops of calcareous rocks.

Montane waterfally spray cliffs. This habitat includes cliffs and underhangs moistened constantly by adjacent waterfalls.

Miscellaneous habitats

Barrier island beaches, dunes, and dune depressions. This habitat includes open habitats of dunes and upper beaches.

Aquatic. This category consists of general emergent, submergent, and floating aquatic freshwater areas.

Tidal. This category includes taxa characteristic of tidal habitats, whether salt, brackish, or freshwater, and including emergent plants of rarely inundated areas and immersed aquatics of permanently flooded estuaries.

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