

DISPERSAL EFFECTS ON SPECIES DISTRIBUTION AND DIVERSITY ACROSS
MULTIPLE SCALES IN THE SOUTHERN APPALACHIAN MIXED MESOPHYTIC
FLORA

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ABSTRACT

Samantha M. Tessel: Dispersal effects on species distribution and diversity across multiple scales in the southern Appalachian mixed mesophytic flora
(Under the direction of Peter S. White)

Seed and spore dispersal play important roles in the spatial distribution of plant species and communities. Though dispersal processes are often thought to be more important at larger spatial scales, the distribution patterns of species and plant communities even at small scales can be determined, at least in part, by dispersal. I studied the influence of dispersal in southern Appalachian mixed mesophytic forests by categorizing species by dispersal morphology and by using spatial pattern and habitat connectivity as predictors of species distribution and community composition. All vascular plant species were recorded at three nested sample scales (10000, 1000, and 100 m²), on plots with varying levels of habitat connectivity across the Great Smoky Mountains National Park. Models predicting species distributions generally had higher predictive power when incorporating spatial pattern and connectivity, particularly at small scales. Despite wide variation in performance, models of locally dispersing species (species without adaptations to dispersal by wind or vertebrates) were most frequently improved by the addition of spatial predictors. Patterns in plant communities were also compared among dispersal categories, and though it was shown that species without dispersal adaptations were less likely to co-occur, this was more likely to be caused by differences in frequency across dispersal categories than by dispersal limitation *per se*. Spatial pattern, distance, and connectivity were significant predictors of non-random patterns of species turnover at all scales and were stronger among dispersal-

limited species groups. Species with limited dispersal were also less frequent at all three sampling scales than those with adaptations for vertebrate dispersal and had smaller geographic ranges than either wind- or vertebrate-dispersed species. Species with no dispersal adaptations were overrepresented among southern Appalachian endemics and lineages endemic to North America, whereas species dispersed by vertebrates were overrepresented among Tertiary disjunct lineages, and species dispersed by spores were cosmopolitan. Relationships among dispersal and biogeographic affinity reflect the evolutionary history of the mixed mesophytic flora owing to adaptation of dispersal mechanisms to regional environmental conditions, the relative ages of lineages, and the effect of dispersal mechanism on the distributions of plants across time and space.

To my family, for fostering in me a love of plants,
to Lucy Braun, who continues to inspire me despite the fact that she died long before I was born,
and to Yontof, who always tried to steal my sedges from underneath the microscope.

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CHAPTER 1. SYSTEMS INTRODUCTION: THE HISTORY AND COMPOSITION OF THE MIXED MESOPHYTIC FORESTS OF THE SOUTHERN APPALACHIAN MOUNTAINS

The southern Appalachian Mountains have long held a mystique among botanists and ecologists as one of the most botanically diverse forest regions of the temperate zone. Botanical exploration of the region dates back to the times of the Bartrams and Andre Michaux, who described the beauty and diversity of the southern Appalachian forests (Core 1970). The southern Appalachians have long been considered a center of diversity for the eastern deciduous forest (Harshberger 1911, Braun 1950, Whittaker 1956). Their topographic heterogeneity, in combination with their unglaciated history, has resulted in a flora rich in endemics, disjuncts, and species of widespread northern affinities (Gray 1878, Braun 1950, Estill and Cruzan 2001). Perhaps the most celebrated and studied forests of the southern Appalachians are the cove hardwood forests, famous for rich soil, lush herb layers, and high species diversity. Considered an example of a mixed mesophytic community, cove forests are characterized by occurring locally in sheltered stream valleys where nutrients accumulate and having a mixed canopy co-dominated by several tree species that thrive in mesic conditions (Braun 1950, Whittaker 1956).

Considering the local richness of nutrients and species in cove forests and a flora often characterized as relictual of a once widespread distribution, it is tempting to assume that environmental effects dominate at local scales and that dispersal and migration are more important at regional scales (Cain 1943, Delcourt and Delcourt 1988). It is important to recognize that plants can be dispersal-limited even on small scales, particularly in a

heterogeneous landscape when appropriate habitats are distributed irregularly in patches.

Dispersal processes can be difficult to measure, especially in the context of steep environmental gradients such as those of the southern Appalachians. I therefore evaluate the importance of dispersal across several scales by focusing sampling on mixed mesophytic cove forests, as environmental variation between sampling locations is reduced, local species richness is sufficient to sample a broad spectrum of dispersal types across several spatial scales, and location along stream drainages allows sampling of several levels of habitat connectivity.

This chapter describes the academic, biogeographic, and developmental history of mixed mesophytic forests, starting with E. Lucy Braun's attempts to characterize, understand, and explain the assembly of mixed mesophytic forests, then by providing a more nuanced description that demonstrates that while Braun's generalizations are useful starting points, the biogeographic history of the flora is much more complicated. I then describe the ecology and composition of mixed mesophytic forests, including dispersal adaptations, endemism, and biogeographic affinities of the flora, and explain how dispersal processes could be important across multiple scales in this system. Afterwards, I describe my sampling of mesophytic forests in the Great Smoky Mountains, present preliminary analyses showing both spatial and environmental trends, and briefly outline the remaining chapters of this dissertation and the questions they address.

The legacy of E. Lucy Braun

A major factor catalyzing the proliferation of studies relating to the distribution of the flora composing mixed mesophytic forests was the publication of E. Lucy Braun's *Deciduous Forests of Eastern North America* in 1950. This work was monumental, not only in describing in detail the floristics of a huge area and its regional variations, but also in connecting the distributions of the flora with current and historical ecological and geomorphic processes.

Braun's brilliance included pioneering phytogeographical analyses of the flora by combining information on current plant species distributions with a knowledge of fossil history, physiography, and ecology to infer the developmental history of a regional flora (Stuckey 1973). A task of such broad scope requires a certain amount of generalization, and though much of Braun's work is remarkably accurate and applicable today, it also relied on some simplifying assumptions based on theories of the time, many of which have been shown to be inaccurate by modern data. Notable among these is Braun's reliance on Clements' (1936) concept of climax communities for mapping and describing regional vegetation and Chaney's (1947) "geoflora" concept to explain the historical development of the eastern deciduous forest.

Mixed mesophytic forest definition

The term "mixed mesophytic" was first used by Braun in her 1914 dissertation to describe forests of the Cincinnati region, but the concept was developed fully in subsequent publications, culminating in her 1950 monograph. She characterizes the mixed mesophytic climax association by a canopy dominated by a mixture of several species including *Acer saccharum*, *Aesculus flava*, *Tilia americana* var. *heterophylla*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Quercus rubra*, *Quercus alba*, *Tsuga canadensis* (now dying), *Castanea dentata* (now dead), *Fraxinus americana*, *Prunus serotina*, *Halesia tetraptera* (in the southern Appalachians), *Magnolia acuminata*, *Betula allegheniensis*, *Betula lenta*, and *Acer rubrum*. Several other species of trees, shrubs, and vines frequently occur in mixed mesophytic forests, and the herbaceous layer is described as unexcelled in diversity and luxuriance (Braun 1950). Braun uses the term 'mixed mesophytic' to describe a plant association, but also designates a particular climax association to a broader region based on a combination of physiographic provinces (*sensu* Fenneman 1938) and the vegetation that characterizes them. Thus, the Mixed Mesophytic Forest

region predominantly corresponds to the unglaciated Appalachian Plateau, though examples of the mixed mesophytic association are not restricted to that region. In the Oak-Chestnut Forest region (which corresponds to Fennemen's (1938) Blue Ridge, Ridge and Valley, and northern Piedmont Provinces), oak-chestnut is considered the climax across the region, but mixed mesophytic is considered "postclimax" due to locally favorable edaphic conditions. Contrariwise, oak-chestnut forests are considered "subclimax" in the Mixed Mesophytic region, where they are restricted to drier ridge tops.

Braun's assumptions

At the time of Braun's research, Clement's (1936) theory of a successional climax community was popular in ecology, and assumed that plant distributions were not independent of one another, but functioned together as units adapted to specific climatic and edaphic conditions. Similar in popularity was Chaney's (1947) "geoflora" concept derived from his interpretation of fossil assemblages, which explained the floristic similarity of eastern North America and east Asia as being relict of an ancestral "Arcto-Tertiary Flora" that was once widespread and homogeneous across the northern latitudes, from which component species migrated southward together as a unit during the later Tertiary. Descriptions of the Arcto-Tertiary Geoflora have a great number of genera in common with Braun's conception of the mixed mesophytic forest, as well as with mesophytic forests of eastern Asia. As such, it is unsurprising that Braun explained the present distribution of plant communities in terms of climatic and regional climaxes, and that she considered the mixed mesophytic forest climax association as the lineal descendent of the Arcto-Tertiary forest (Braun 1950, 1955). She also considered most other climax associations of the eastern deciduous forest to be derived from the more diverse mixed mesophytic forest, as most species therein either also occur in mixed mesophytic communities or have relatives that

do. Braun attempted to connect the development and spatial distributions of forest regions with landscape evolution through Davis's idea of erosion cycles in geomorphology (Wright 1974) and to Fennemen's (1938) description of physiographic regions, in particular associating the mixed mesophytic forest with the Schooley peneplain and areas of diverse topography (Braun 1947, 1950, 1955). The peneplain model for the Appalachian Mountains, though not necessarily wrong, has become largely obsolete due to limited evidence for peneplains in the Appalachians and a more recent focus on process geomorphology and plate tectonics (Sevon et al. 1983, Hatcher et al. 1989, Oldroyd and Grapes 2008). Furthermore, Braun's attempt to connect the current distribution of mixed mesophytic forests with erosion cycles assumes that the mixed mesophytic forest has persisted in situ, virtually unchanged since the mid-Tertiary, and that Pleistocene glaciations had minimal effect on vegetation and plant species distributions south of the glacial boundary. This hypothesis was based on an intimate knowledge of modern species distributions, as fossil data from both the Tertiary and Quaternary periods is fairly rare in the eastern United States (Braun 1950, 1955). Our understanding of the complexities of composition, geography and history of the mixed mesophytic forests has increased substantially since Braun's work on the subject, though she laid the foundation for a modern and holistic perspective. The frameworks she used often remain useful descriptors of broader trends in vegetation patterns, but it is important to note their limitation. The overarching trend in our modern understanding is that every species has its own dispersal history and its own ecological limitations, such that plant communities are not discrete entities, but vary through time and space.

Climax communities

Though Gleason (e.g. 1926) long ago argued against the concept of a climax plant community in favor of a spatially variable one in which species respond differently to

environmental conditions and which species composition depends on available migrants, his 'individualistic' concept of the plant association was largely dismissed by ecologists of the time (McIntosh 1975). It has since been shown that species are distributed largely independently on environmental gradients and that species composition and diversity are limited by dispersal processes (Whittaker 1956, Matlack 1994). Within mixed mesophytic forests of the southern Appalachian Mountains in particular, Whittaker (1956) found that tree species are distributed independently on an elevation gradient, and that whereas Braun (1950) differentiated cove hardwoods of lower elevations and "northern hardwood" forests of higher elevations as discrete communities, community composition among cove and northern hardwoods actually changes continuously such that they are inseparable on mesic sites. Whittaker's (1956) analysis of vegetation of the Great Smoky Mountains also suggests that Braun's (1950) concept of the mixed mesophytic forest bears closer resemblance to a diverse community transitional between cove hardwood forests and montane oak forests. Despite dispersal limitation and independent environmental distributions, and despite the fact that plant community composition depends not just on geomorphology but also on soil parent material and edaphic conditions, the concept of a regional climax is nonetheless a useful framework for mapping of dominant vegetation (Braun 1950, Gleason and Cronquist 1964, Howard and Mitchell 1985, Hinkle et al. 1993). More recent studies based on statistical analysis of tree species composition have shown that though Braun's mapping of the boundaries between forest regions is remarkably accurate, there is no clear boundary vegetation boundary between the regions she delineates as Mixed-Mesophytic, Western Mesophytic, and Oak-Chestnut, and that individual tree species are distributed across spatial and environmental gradients (Delcourt and Delcourt 2000, Dyer 2006).

Tertiary geoflora

Ideas about climax plant communities were echoed in the paleobotanical literature with Chaney's (e.g. 1947) concept of widespread homogeneous geofloras that migrated as cohesive units in response to climatic changes of the Tertiary. The idea emerged from the Chaney's development of the concept of an "Arcto-Tertiary Flora" that was widespread and homogeneous across northern latitudes in the early Tertiary, an attempt to connect fossil history, the modern floristic relationship between eastern North America and east Asia, and Clementsian ideas about climax communities (Wolfe 1977, Tiffney 1985). The term "Arcto-Tertiary" was first used by Engler in reference to elements of the north temperate forest flora with ancestors in the Arctic region during the Tertiary, but conceptually dates back to the works of Asa Gray on the floristic affinities between eastern North America and eastern Asia (Gray 1878, Engler 1882). Gray was not the first to note the relationship, but was the first to put forth a well-developed hypothesis on its origins based on extensive knowledge of generic and species distributions (Boufford and Spongberg 1982, Tiffney 1985). Gray hypothesized that temperate forests and many of their component taxa had a biogeographic connection across the arctic during the Tertiary, that there was subsequent extinction of deciduous trees in western North America, and that the east-west trending mountains in Europe cut off access to southern refugia for many species during glaciation (Gray 1878). The accumulation of floristic and fossil evidence has since largely confirmed Gray's hypothesis and has led to the association of floristics of northern hemisphere temperate forests with historic forests of the Tertiary (Graham 1972, 1999). The cove forests of the southern Appalachian Mountains in particular were noted for the large proportion of genera shared with fossil floras from the northern hemisphere Tertiary, disjunct between eastern North America and East Asia, or both (Cain 1943). Braun's association of the mixed mesophytic forest

with Chaney's conception of an Arcto-Tertiary Flora has resulted in the application of the term "mixed mesophytic" not only to many Tertiary fossil floras of mixed species composition but also to extant floras in eastern Asia dominated by many genera shared with the mixed mesophytic forests of North America (Wang 1961, Graham 1999).

Modern understanding of vegetation history

We now know that the "mixed mesophytic forests" of eastern North America and eastern Asia, though sharing many genera, are neither the same climatically nor physiognomically (Wolfe 1979), that temperate forests of the northern hemisphere Tertiary were far from homogeneous in species composition, and that elements of current mixed mesophytic forests migrated independently rather than as a unit (Graham 1972, 1993, 1999; Wolfe 1972, 1977). The concept of an Arcto-Tertiary Flora is useful as a very general explanation for the widespread temperate flora across the northern hemisphere Tertiary and for the disjunctions between many components of the flora of eastern North America and eastern Asia, but it confounds vegetation structure and species composition (Wolfe 1972, 1977, Tiffney 1985). Fossil evidence suggests that though temperate elements were widespread across high latitudes in the early Tertiary, they were often mixed with tropical elements, and that many of the taxa of the temperate mixed mesophytic forests are descended from tropical relatives that migrated from Southeast Asia across the Arctic to North America (Wolfe 1975, 1977). Some of the morphological similarities in taxa disjunct between the two regions is due to morphological stasis over a long period of time in fairly stable ecological conditions (Wen 1999). In addition, both fossil and molecular and biogeographic evidence show that many of the lineages that now exhibit the "classic" eastern North America-eastern Asia disjunction diverged at varying times, again indicating independent dispersal histories (Tiffney 1985, Tiffney and Manchester 2001, Xiang and Soltis 2001,

Donaghue and Smith 2004). The current species composition of mixed mesophytic forests of the southern Appalachian Mountains predominantly results from the complex history of the Tertiary, during which each component species had its own evolutionary and distributional history. It is necessary, however, in order to understand the development of the flora, to understand also the changes in vegetation as a whole as a context within which to place evolution, divergence, and migration of individual taxa.

During the late Cretaceous a large epicontinental sea separated eastern and western North America with little floristic interchange. Macrofossils from this time are generally difficult to attribute to taxonomic group, but the physiognomy of leaf deposits suggest that eastern North America had tropical forest vegetation, western North America had largely subtropical forests, and northern areas graded into polar deciduous forests. Some of the families represented by late Cretaceous tropical floras of the southern Appalachians include Taxodiaceae, Juglandaceae, Platanaceae, Fagaceae, Aceraceae, Theaceae, Magnoliaceae and Ebenaceae. The bolide impact at the end of the Cretaceous resulted in atmospheric debris, decreased photosynthesis, and reduction of global temperature, possibly facilitating the spread of deciduousness among many plant groups (Graham 1999).

Climate warmed throughout the Paleocene, reaching a Tertiary maximum in the early Eocene. During this time, the epicontinental seas of the Cretaceous had receded, and tropical forest had spread throughout the southeastern United States, while the Appalachian Mountains had temperate elements including *Betula*, *Carya*, and *Ilex* (Graham 1993, 1999). Meanwhile there were land connections between the old and new worlds across Beringia and the North Atlantic, facilitating biotic interchange of both temperate and tropical taxa through the Eocene. The Eocene flora of high latitudes most closely approximates the concept of the Arcto-Tertiary

Geoflora, with the caveat that there was a large tropical element to the flora and fossil assemblages are not spatially homogeneous (Wolfe 1972, 1977). The number of genera that are today attributed to mixed mesophytic forests dramatically increased in the Eocene high latitudes, which also included taxa currently restricted to Asia, such as *Metasequoia*, *Ginkgo*, *Cercidiphyllum*, and *Platycarya*. Greenland was a bit farther south than Beringia at the time so it is likely that the North Atlantic connection between Europe and eastern North America during the early Eocene facilitated movement of more tropical lineages than across northeastern Asia and Alaska (Tiffney 1985, Tiffney and Manchester 2001). Vegetation across the middle latitudes in North America was largely subtropical, grading to more temperate at higher elevations in the Appalachian Mountains. The southeastern flora of the middle Eocene then contained *Nyssa*, *Fraxinus*, *Tilia*, *Symplocos*, *Corylus*, *Juglans*, *Castanea*, *Fagus*, *Celtis*, and *Ulmus*, as well as members of the Annonaceae, Fabaceae, Araliaceae, Cyrillaceae, Lauraceae, and Araceae (Graham 1993, 1999).

Cooling, drying, and more seasonal rainfall across North America from the middle Eocene onwards caused by the uplift of the Rocky Mountains resulted in expansion of warm-temperate deciduous vegetation in the Southeast and the precursors of modern mixed mesophytic forest associations. By the Oligocene, northern latitudes were predominantly deciduous, and the terrestrial link across the North Atlantic Land Bridge was broken. Climate fluctuated through the Oligocene and Miocene but gradually cooled, and continued uplift of the Rocky Mountains resulted in drying and development of grasslands in the continental interior, disproportionate extinction of broad-leaved deciduous trees in the western United States, but expansion of mixed mesophytic forests across eastern North America (Graham 1993, 1999). During this time, the Bering Land Bridge was open for plant migration, and some genetic evidence suggests that

temperate plants also may have been able to migrate across the North Atlantic (Wen 1999, Tiffney and Manchester 2001). Though fossil evidence for herbaceous taxa is sparse, it is likely that many originated, spread, and diversified during the Miocene as understory plants in the mixed mesophytic forests (Tiffney 1985). Genetic and biogeographic evidence suggests that many of the taxa of Tertiary disjunct distributions diverged during this time, including *Caulophyllum*, *Asarum*, *Aralia*, *Phryma*, *Calycanthus*, *Liriodendron*, and *Cornus* (Tiffney and Manchester 1999, Wen 1999). By the end of the Miocene both the aspect and composition of mixed mesophytic forests were essentially modern.

Climate continued to cool through the Pliocene, and uplift of additional mountain ranges in western North America contributed to the dominance of conifers in western montane forests and expansion of desert and grasslands. The expansion from the west of drier ecosystems, in combination with the closure of the Isthmus of Panama, likely facilitated infiltration of mixed mesophytic forests by genera from families more frequent in drier habitats and without biogeographic affinities with eastern Asia or northern temperate forests, such as Asteraceae and Lamiaceae (Tiffney 1985, Singh 1988, Graham 1993). The overall cooling throughout the later Tertiary resulted in the extinction of many Asian and tropical elements from the southeastern flora, as well as the formation of high-elevation coniferous forests in the Appalachian Mountains (Graham 1993, 1999).

Pleistocene glaciations predominantly resulted in the reshuffling of the flora of the southeastern United States, though without causing many extinctions due to continuous habitat along the north-south trending Appalachian Mountains and refugia along river bluffs of the southeastern coastal plain (Delcourt and Delcourt 1975, 1984). While Braun (1955) maintained that the mixed mesophytic forest south of the glacial boundary remained largely intact during the

Pleistocene, evidence from the pollen record suggests that vegetation throughout the southeastern United States changed substantially, with temperate forests largely displaced by boreal forests (Jackson et al. 2000). Fossil evidence again suggests that species had individualistic responses to climate change and separate migration histories, such that many plant communities of the Pleistocene have no modern analogue, and the species making up mixed mesophytic forests did not all find refugia in the same areas (Davis 1983, Williams et al. 2004). Though the pollen record says little about herbaceous species, tree species of mixed mesophytic forests largely shifted southwards, though varying in both location of primary glacial refugia as well as timing of post-glacial recolonization (Decourt and Delcourt 1983, Williams et al. 2004). Many species appeared to recolonize northwards from coastal plain refugia after glacial retreat (Davis 1983, Delcourt and Delcourt 1987). These were likely located along river bluffs with rich soil and moderate climate, such as the Tunica Hills along the Lower Mississippi River in Louisiana, the Apalachicola River Bluffs in the Florida panhandle, and the Savannah River on the southeastern Atlantic coastal plain. These rivers are postulated to be migrational pathways between the southern Appalachian Mountains and the southeastern coastal plain for mixed mesophytic taxa, as they provide continuous habitat for deciduous forests species due to topographic relief and edaphic conditions, and all are noted locations for the southernmost extent or relictual distribution of many taxa characteristic of mixed mesophytic forests (Delcourt and Delcourt 1975, Weakley 2015). Despite the fact that the pollen record suggests displacement of tree taxa southward, recent molecular evidence shows that certain mixed mesophytic taxa likely had populations that persisted in the southern Appalachian Mountains during times of glaciation (McLachlan et al. 2005, Gonzales et al. 2008).

Dispersal and migration

Post-glacial migration

Braun (1950, 1955) posited that the patterns of endemism in the southern Appalachian Mountains could only be explained if mixed mesophytic forests persisted in local protected areas during glaciation, and haven't yet expanded northward into appropriate habitat in previously glaciated territory. Delcourt and Delcourt (1988), however suggest that cove hardwoods could not have persisted locally through the Pleistocene because of landscape instability associated with periglacial processes. Though it is true that mesophytic species without morphological adaptations for long distance dispersal have shorter dispersal distances and are more likely to be southern Appalachian endemics, studies analyzing dispersal distances and the time since glacial retreat show that many species with limited capacity for dispersal have spread northward into glaciated regions faster than expected, even assuming refugia close to the glacial boundary (Cain et al. 1998). Recolonization rates varied among the many species of mixed mesophytic forests depending on locations of multiple refugia, dispersal strategy, differential response to climate change, habitat, habitat connectivity, and chance historical and long-distance dispersal events (Davis 1983, Delcourt and Delcourt 1983, 1984, Cain et al. 1998, Clark et al. 1998).

Dispersal morphology and biogeography of mixed mesophytic forest species

Today, we perceive the species composition of mixed mesophytic forests of the southern Appalachians to be a product of both current and historical processes relating both to individualistic responses to environmental gradients and dispersal across landscapes and regions. Dispersal morphology is largely an adaptation to local environment, the abundance of seed dispersal agents, and life history traits, but also affects the local and regional distribution of taxa (van der Pijl 1969, Howe and Smallwood 1982, Willson and Traveset 2000, Bullock et al. 2002).

Dispersal by winged seeds, for example, is common among temperate canopy trees, and allows them to recolonize canopy gaps quickly (Brokaw and Busing 2000, Bullock et al. 2002).

Dispersal by fruit/seed ingestion is most common among shrubs, small trees, and vines, likely due to the abundance of birds and mammals living in the forest understory (Hinkle et al. 1993).

Most herbaceous species of mixed mesophytic forests, however, have no obvious dispersal adaptations, though many of the more common ones are dispersed by ants, vertebrates, or spores (Beattie and Culver 1981, Handel et al. 1981, Whigham 2004). Localized dispersal is thought to be an advantage in stable habitats such as the sheltered mountain coves, where the plant species adapted to such conditions would be able to persist across multiple generations rather than spreading seeds farther across inhospitable habitats (van der Pijl 1969, Levin et al. 2003, Snyder and Chesson 2003, Clobert et al. 2012). In turn, dispersal capacity affects the local, regional, and biogeographical distributions of taxa. Among mesic forest herbs, recolonization after a disturbance from non-local sources is more likely among species with adaptations for animal dispersal (Thompson 1980). At landscape scales, forest destruction and fragmentation increase the likelihood that species without adaptations for long distance dispersal will be absent or rare in smaller or second-growth forest patches (Matlack 1994, Pearson et al. 1998). Dispersal morphology even affects the broad scale distribution of species and higher taxa, where species without adaptations to long-distance dispersal are more likely to be southern Appalachian endemics, and are underrepresented among genera of Tertiary disjunct affinities, despite their theoretical adaptation to the stable environments that characterize the biogeographic history of mixed mesophytic forests (Wen 1999). The biogeographical affinities of the flora of the mixed mesophytic forest vary as a function of the location and timing of origin of taxa, their ecological tolerances, and the history of their migration. Most tree genera of the mixed mesophytic forests

of the southern Appalachians are either widespread north temperate or restricted to eastern North America and eastern Asia. Herb genera are more evenly divided between cosmopolitan, north temperate, Tertiary disjunct, and North American endemic. Altogether, approximately 25% of the genera of cove forests are widespread north temperate in distribution, 30% are tertiary relicts, 25% are endemic to North America (most of which are restricted to eastern North America), and 25% are mostly cosmopolitan. Of all species, more than 12% are endemic to the southern Appalachian Mountains (Appendix 2).

The distribution of mixed mesophytic forest species in the southern Appalachians

In the southern Appalachians, mixed mesophytic forests are found in areas rich in moisture and nutrients. Most typically, these areas are located in protected stream valleys (coves) on cool, north-facing slopes where soil moisture is high and nutrients accumulate, but many of the same species occur in other mesic areas or areas of high soil fertility, such as somewhat dryer slopes underlain by mafic or calcareous rock, or higher elevation areas with mesic soils due to high precipitation and cooler climate. Many cove forests contain boulderfields at medium to higher elevations as a result of Pleistocene periglacial processes (Schafale and Weakley 1990, Ulrey 2002). Elevation, landform, aspect, and underlying geology all affect species differently in mesophytic forests, contributing to the compositional gradient between rich cove forests, northern hardwood forests, boulderfield forests, and montane oak forests with rich soils (Schafale and Weakley 1990, Schafale 2012). Despite some compositional change along environmental gradients, mixed mesophytic forests of the southern Appalachians are an ideal system in which to study issues of dispersal and habitat connectivity in natural landscapes, as they are primarily distributed along stream drainages, which show varying degrees of connectivity as higher-order streams converge at lower elevations. Holding habitat relatively

constant in addition to conducting surveys of such a diverse system with an extensive biogeographic history allows analysis of the effects of dispersal on the local and regional floristic composition across several scales of space and time.

Inferring dispersal in natural communities

In this dissertation I use the mixed mesophytic forests of the southern Appalachians as a study system in which to investigate the effects of dispersal across multiple scales. As dispersal processes are difficult to measure directly in natural systems, I address dispersal by contrasting patterns between groups of species differing in morphological adaptations to dispersal agents. Because dispersal is a distinctly spatial process, I use spatial proxies while controlling for environmental variation to indicate the importance of dispersal in structuring the composition of mixed mesophytic forests. In addition, because plants disperse across space over multiple generations, and because habitats suitable for mixed mesophytic species are often local and spread irregularly across a heterogeneous landscape, I use several levels of habitat connectivity to characterize the interaction between dispersal processes and environmental conditions. I address issues of scale by using a nested sampling scheme ranging from sample sizes of 0.01 to 1 hectare as well as by including analyses focusing on both local and regional species distributions and landscape scale community composition.

Sampling mixed mesophytic forests

Plant communities of the southern Appalachian Mountains often vary gradually along gradients of elevation, moisture, and geology to the point where cove hardwoods, "northern" hardwoods, and oak forests are compositionally indistinct in mesic and nutrient-rich environments (Whittaker 1956, Schafale 2012). To capture this variation, I targeted sample locations in Great Smoky Mountains National Park mapped as rich cove, red oak cove, rich

northern hardwood, or boulderfield forests (White et al. 2003, Madden et al. 2004). I prioritized sampling in large areas with fairly homogeneous species composition where I could sample several hectares in the same habitat patch, or else place additional hectare plots in the same network of patches or watershed. The vegetation map for the park is subject to some error in vegetation classification, but was useful as a tool to target potential sample locations and understand their spatial relationships with nearby vegetation (Madden et al. 2004, Jenkins 2007). I therefore verified that community composition fit moderately well with one of the primary communities listed in Appendix 1, and contained several rich mesophytic indicator species (indicated in Appendix 2). I assigned several levels of habitat connectivity based on the vegetation map, stream drainage systems, and personal observation. Based on the vegetation map and accuracy assessment of Madden et al. 2004 and Jenkins 2007, two habitat patches were considered in the same network if they were connected by intervening habitat that was marginally appropriate for mesic species, but not particularly nutrient rich (secondary communities in Appendix 1). These communities share many species with mixed mesophytic forests, but the rich mesophytic indicator species indicated in Appendix 2 are generally rare or absent. In addition, because mesic habitat along streams connects patches of mixed mesophytic forests, I used stream, small river, and large river watersheds as additional variables representing successively broader scales of habitat connectivity. Overall, 47 1-hectare study sites were sampled across eleven watersheds. Distance between hectares ranged from greater than 100 meters to almost 60 km, and elevation ranged from 500 to 1400 meters (Figure 1.1). All plant species were recorded in each hectare, yielding a combined total of 396 species (Appendix 2). Preliminary analysis of the dataset in relation to environmental variables measured using Geographic Information Systems and soil sample analysis showed that hectare species

composition is related to environmental gradients, but that species composition also shows strong spatial trends by watershed (Figures 1.2 and 1.3). My analyses focus on discerning the spatial trends related to environmental gradients from those emerging from dispersal limitation among patches of mixed mesophytic forest, and on associating the distribution of species of mixed mesophytic forests of the southern Appalachian Mountains with current and historical dispersal processes.

Analysis of scales of dispersal importance in mixed mesophytic forests

Braun's (1950, 1955) comprehensive descriptions and phytogeographic explanations for the composition and distribution of the mixed mesophytic forest remain a landmark in botanical ecology and biogeography, and are largely valid today, with the predominant exceptions being her lack of emphasis on individualistic elements of the flora and processes of dispersal and migration. This dissertation builds upon her work by emphasizing the exceptions to general trends in the distribution and composition of mixed mesophytic forests being governed purely by environmental conditions, focusing instead on how dispersal processes affect composition across multiple scales. In the following chapters, I use measures of spatial relationships, habitat connectivity, and dispersal morphology to reveal patterns in the species composition across several scales in mixed mesophytic forests of the southern Appalachians that are structured by dispersal.

I here present five chapters aimed at understanding how dispersal processes manifest at a variety of scales. Chapter 2 first defines five relative spatial scales based on how dispersal is expected to interact with levels of spatial heterogeneity of environmental conditions, then reviews methodology in the study of plant dispersal and the scales at which they are appropriate and practical. Chapters 3-5 use a sampling of the methodology described in Chapter 2 to assess

the importance of dispersal processes to species distribution and community composition. Chapter 3 asks whether spatial predictors improve species distribution models based on environmental variables, and whether model performance depends on scale or dispersal mechanism. Chapter 4 evaluates non-random patterns in community composition, whether they are affected by spatial limitation independent of environmental variables, and how they are affected by dispersal mechanism and scale. Chapter 5 takes a macroecological approach to evaluate differences in range, frequency, and biogeographic affinity between dispersal mechanisms. Finally, Chapter 6 synthesizes the ways in which dispersal processes are important in affecting diversity of mesophytic forests across many scales.

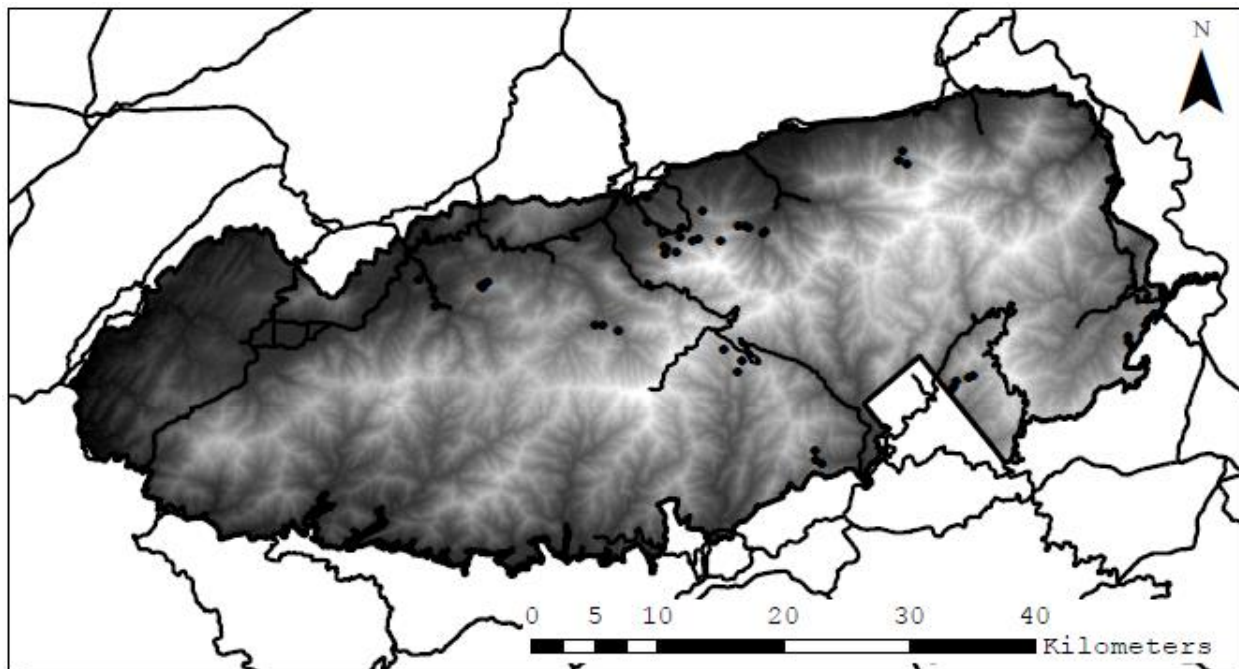


Figure 1.1. Sampling locations in Great Smoky Mountains National Park. Shading shows a digital elevation model of the park (NPS 2011), where lighter values indicate higher elevation. Lines indicate major roads and park boundaries.

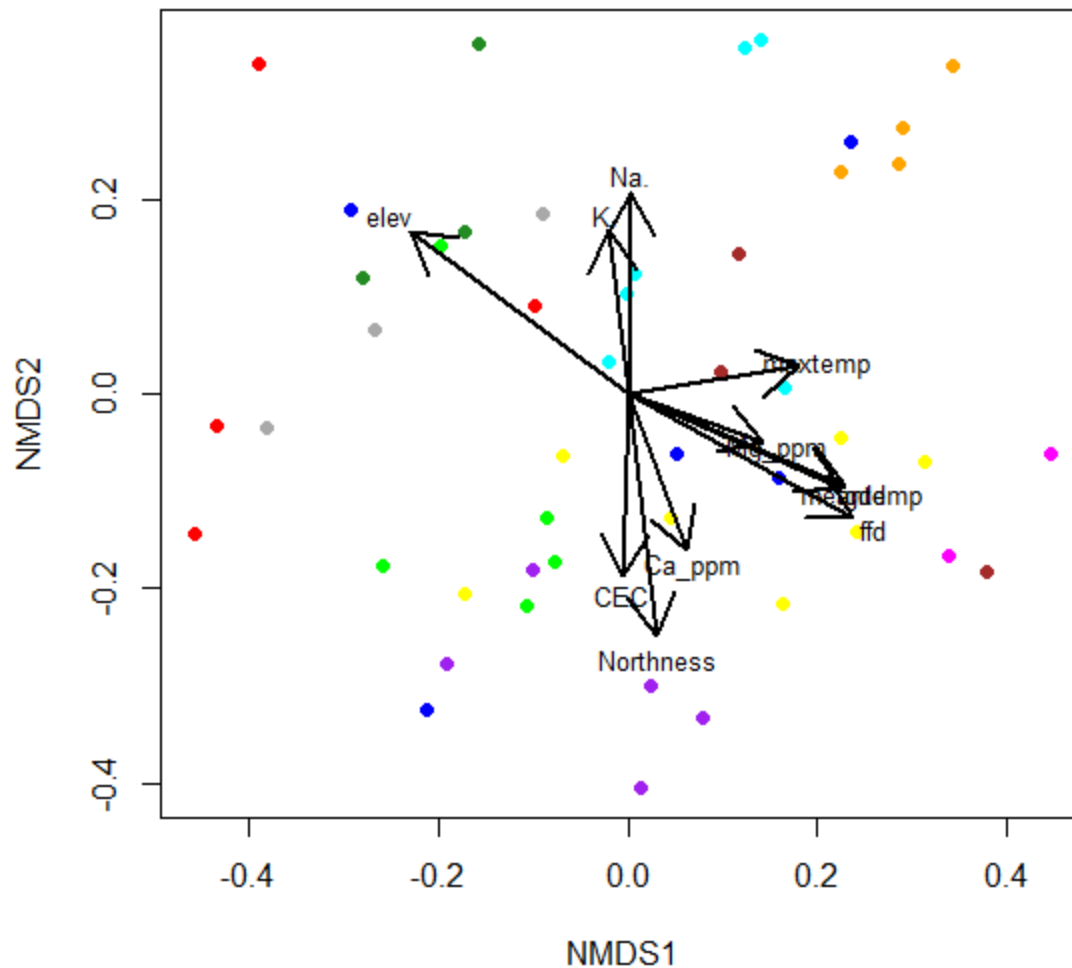


Figure 1.2. Non-metric Multidimensional Scaling showing results on the first two of four axes (stress 0.18, $R^2=0.71$). Axis one is strongly correlated with elevation (elev) and temperature parameters (maxtemp, meantemp, ffd, gdd) and explains 28% of the variation in Jaccard dissimilarity, while axis two is correlated with transformed aspect (Northness), Cation Exchange Capacity (CEC), and micronutrient availability including calcium (Ca_ppm) and magnesium (Mg_ppm), and explains 8% of the variation in changes in community composition. Colors represent stream watersheds.

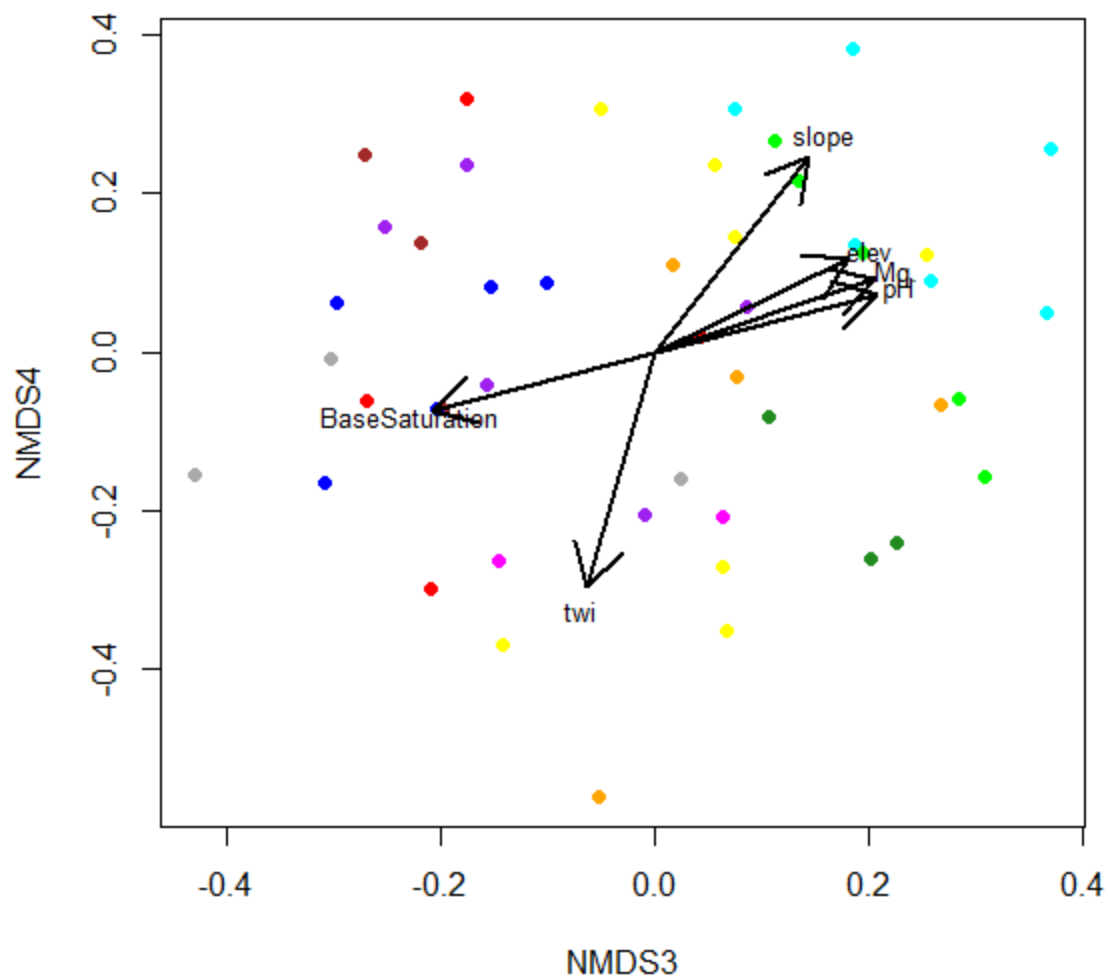


Figure 1.3. Non-metric Multidimensional Scaling showing results on the second two of four axes (stress 0.18, $R^2=0.71$). Axis three is correlated with pH and base cation saturation (BaseSaturation) and explains 4% of the variation in Jaccard dissimilarity, while axis four is strongly correlated with slope and topographic wetness index (twi), and explains 15% of the variation in changes in community composition. Colors represent stream watersheds.

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CHAPTER 2. EVALUATING THE EFFECTS OF DISPERSAL PROCESSES ON PLANT SPECIES DISTRIBUTIONS AND DIVERSITY ACROSS MULTIPLE SCALES: A REVIEW AND SYNTHESIS

Introduction

Dispersal processes have come to the forefront of ecology as a way of placing ecological interactions in a spatially explicit context (Bullock et al. 2002, Levine et al. 2003, Ricklefs 2008, Clobert et al. 2012). One of the short-comings of this research has been the importance of dispersal has been quantified predominantly in context-specific way, with results that are dependent on the focal organisms, scale, and spatial context of the study (Murphy and Lovett-Doust 2004, Jacobson and Peres-Neto 2010). Furthermore, dispersal processes are intimately linked with ecological interactions in ways that manifest differently across spatial scales, such that it is empirically difficult to separate one from the other (Leibold et al. 2004). This is hardly surprising, as pattern in ecology is often spatially contingent and scale-specific, but it is a particular challenge for plants as passive dispersers whose survival and reproduction is dependent on habitat quality, and which cannot simply move to more appropriate habitat. This generates feedback, where spatial pattern can emerge because of restricted dispersal and environmental constraints, but the spatial configuration of habitats in turn affects history and probability of colonization. Another challenge is that it is difficult to directly measure the frequency distribution of dispersal distances at all but fairly narrow spatial scales, so discerning the contribution of dispersal limitation from environmental control of plant species distributions relies on various proxies such as spatial relationships and dispersal vectors, as well as the

assumption that all pertinent environmental variables affecting plant distribution have been measured (Greene and Calogeropoulos 2002, Jacobson and Peres-Neto 2010).

In this chapter, I first synthesize the roles of dispersal and colonization in determining distribution patterns of plants across multiple scales, and then review potential methodology for assessing the importance of dispersal. Dispersal affects the composition of natural vegetation across spatial scales ranging from local to worldwide and across levels of biotic organization ranging from populations to floras. Because scales of ecological interaction are relative due to differences between species in size, life history traits and habitat specificity, it is necessary for the purposes of discussion first to define characteristic scales for plant spatial relationships. Rather than using absolute scales and assuming that each species responds similarly to particular dimensions of spatial heterogeneity, the first section discusses the complexities involving issues of scale with regards to plants, and defines five relative scales based on relevant spatial and ecological processes. I then use the second section to review methods with which dispersal processes can be quantified or inferred. The goal of this chapter is to summarize how dispersal processes relate to spatial scale, then to choose several appropriate strategies with which to identify the importance of dispersal across many scales for patterns of quantification of natural distribution and diversity in plants. The selected approaches are then employed in the following three chapters for the flora of mixed mesophytic forests in the southern Appalachian Mountains.

Scales of dispersal processes

Every ecological interaction is contingent on spatial relationships. Five typical examples of the importance of spatial relationships and scale are: 1) proximity of individuals of the same species contributes to the structure of metapopulations (Hanski 1998); 2) competition among individuals within and across species for limiting resources depends on neighborhood

interactions (Addicott et al. 1987); 3) resource availability is spatially correlated and scale dependent (Legendre 1993); 4) the probability of local occurrence of species and communities is influenced by landscape configuration of habitat patches (Chase 2003); and 5) regional diversity is linked to geographic trends in speciation and dispersal within and between regions (Ricklefs 1987, 2004). Spatial heterogeneity in resources and habitats across many scales presents a particular challenge for sessile organisms such as plants that can only traverse space across more than one generation: dispersing propagules either establish locally or they do not; it is therefore essential for understanding population, metapopulation and species persistence that plants disperse their propagules across a range of distances (Addicott et al. 1987).

Plant distribution and diversity patterns are produced when dispersal processes intersect with scales of environmental heterogeneity. Different plant species experience patchiness at various scales, depending on their size, habitat specificity and on the likelihood of dispersal, so absolute scales are arbitrary and context-specific. Most ecologists get around this problem by using relative terminology when discussing issues of scale (e.g. local versus regional, small versus large, narrow versus broad) and assume that others have similar definitions. Below, I begin by further discussing the complexities inherent in plant dispersal, the relationships between spatial and temporal scale, and the local-regional dichotomy. I then present a different approach in which I use the various processes that drive patterns of plant distribution to assign a functional definition of scales that is both hierarchical and flexible.

Spatial pattern and dispersal

Plant species use various strategies and adaptations for colonization. The most obvious are adaptations for seed dispersal such as winged seeds, edible fruit, and elaiosomes, but characteristics that affect metacommunity abundance may also play a large role in determining

the probability that any given location is colonized by a particular species (Hubbell 2001). This may include life history traits such as fecundity and life span as well as habitat specificity. In addition, characteristics of the landscape itself may affect each species differently, as each species has different combinations of dispersal syndromes, habitat optima and specificity, and the abundance and connectivity of appropriate habitat varies by species and landscape (Addicott et al. 1987, Levin 1992). Furthermore, historical influences affect the spatial patterns of species distributions as past local and regional extinctions may restrict some species to smaller and more local portions of their potential ranges.

Space and time interaction

The spatial scale of autocorrelation in plants is necessarily related to temporal scale, because 1) the frequency of propagule dispersal is generally inversely related to distance from the parent plant (e.g. Clark et al. 1998b), and 2) the spatial scale of ecological events and processes is positively correlated with temporal scale (e.g. Delcourt et al. 1983, Urban et al. 1987). The probability of a chance, long-distance dispersal event is influenced by adaptations such as seed or fruit morphology as well as propagule mass. Many species have multiple dispersal vectors, and the relative importance of different vectors is likely to vary across spatial scales (Nathan 2006). Recruitment of plants at any spatial scale is constrained first by the arrival of propagules, and then by ecological interactions. Conversely, seed rain depends on the spatial proximity of established individuals, which results from the distribution of appropriate habitat and colonization history. What is considered 'appropriate habitat' for an individual varies by species and is scale-dependent spatially according to the ratio of the size of the individual to the size of the microhabitat, and temporally according to the ratio between the time from germination to successful reproduction and the temporal persistence of suitable environmental

conditions (Levin 1992). The interaction between dispersal and ecological processes that determines occurrence, abundance, and spatial distribution of plant species depends on the frequency distribution of distances traveled by propagules ('dispersal curve') as well as various environmental and ecological parameters depending on spatiotemporal scale.

The local-regional dichotomy

In an attempt to unite the historically disparate frameworks of community ecology and biogeography, ecologists have increasingly viewed ecological processes such as competition, predation, and niche relationships as "local processes", and biogeographic processes such as dispersal, history, and speciation as "regional processes", with the implication that there are primarily two scales of interest wherein the former is dominated by "deterministic processes" and the latter by "stochastic processes" (Chase and Myers 2011, Huston 1999, Cornell and Lawton 1992, Ricklefs 1987, 2004). While these assumptions are quite rational because of both the impossibility of competition without spatial interaction and the fact that dispersal limitation increases with spatial scale by definition due to dispersal curves, they are also overly simplistic because: 1) stochastic dispersal events influence local community composition (Bullock et al. 2002, Chase 2003); 2) other "local processes" including demography and disturbance are often stochastic (Hanski 1996, Pickett 1980, Pickett and White 1985); and 3) "regional processes" such as speciation and range expansion can have a deterministic element due to environmental control of speciation rate and competition between species influencing range limits (MacArthur 1972, Ricklefs 2004, Wiens 2011). As to whether dispersal is a "stochastic process", it is certainly not random in space, and because different species have different adaptations to dispersal, colonization, and life-history tradeoffs, it is also nonrandom among species (Adler et al. 2007). Also, as discussed above, "local" and "regional" mean different things when applied to different

species, depending on their life histories, dispersal curves and scales of response to environmental heterogeneity (Addicott et al. 1987, Levin 1992). The scales delineated below are based not on a threshold of dominance between deterministic and stochastic processes (e.g. Chase and Myers 2011), or on the assumption that dispersal limitation is a process operating on primarily broad scales (e.g. Shmida and Wilson 1985, Ricklefs 1987), but rather on variation in distribution and diversity patterns that may be produced when scales of environmental heterogeneity interact with dispersal probability. As such, this framework is flexible with regard to species and assemblages, and can be used conceptually to inform appropriate sampling scales and methods for detecting the role of dispersal in creating spatial patterns of plant species distribution and diversity.

Characteristic scales of heterogeneity

Below, I recognize five relative and nested scales of environmental heterogeneity based on plant response. Survival and successful reproduction of any individual plant depends on the amount and timing of available resources, which are patchily distributed in space and time across multiple scales. The area that includes an individual plant and the resources it uses is a microsite (Eriksson and Ehrlén 1992). Microsites with similar environmental conditions (microhabitats) are often spatially correlated, and microhabitats with varying combinations of resource availability are often co-distributed because of a common underlying process (e.g. nutrient accumulation, erosion, disturbance) or broader-scale environmental variable (e.g. slope, aspect, geology) defining a habitat patch suitable for many species that frequently co-occur. A habitat patch is therefore often characterized by some degree of homogeneity of community composition (Pickett and White 1985, Huston 1999). Habitat patches may be clustered or arranged randomly or regularly within a landscape, depending on the spatial distribution of the variables or

processes that define habitat (Forman and Godron 1981). What is often defined as a region is larger than a landscape, and is characterized by some degree of homogeneity in climate, geomorphology and species distributions. Thus, my first four characteristic scales defined by plant distribution correspond to areas the size of a microsite, habitat patch, landscape, and region, though the absolute dimensions of each of these varies depends on species and context. The broadest scale, biogeographic scale, spans more than one region.

Neighborhood scale

At very narrow spatial scales, neighboring plants may compete with each other for space and accessible resources (Pacala 1986, Tilman 1994), however the specific identity of individuals competing is at least in part determined by seed rain, which is often highest close to the parent plant (Greene and Calogeropoulos 2002). This may result in clustering at small scales, where individual plants are more likely to be surrounded by conspecifics than any other species, thereby reducing the ratio of interspecific to intraspecific competition and producing a stabilizing effect at the population level (Chesson 2000, Holyoak and Loreau 2006). Small-scale clustering may also result in Janzen-Connell effects, where predation and pathogens may disproportionately affect plants in conspecific clusters, thus possibly resulting in overdispersion of seedlings at small lag distances (Levine and Murrell 2003). The underlying assumption of such models of clustering or overdispersion is that the same microsite is suitable for multiple species. The spatial scales at which such processes as local dispersal, resource competition, and Janzen-Connell effects occur can be termed neighborhood scale because such processes predominantly operate at the relatively short distances of interacting individuals (Addicott et al. 1987).

Habitat scale

At slightly larger distances from parent plants, seed rain is more stochastic, and the exact timing of seed rain at a microsite may result in priority effects within a larger habitat patch; if seeds from multiple species fall in the same area, the first species to germinate and establish may have a better chance at monopolizing available space and resources, thus preventing subsequent invasion. This may be related in part to demographic and life history traits affecting growth rate, fecundity and dormancy, but is also stochastic owing to chance arrival of propagules to a microsite from the community at large (Grubb 1977). Similarly, models of lottery competition may apply when a microhabitat suitable for more than one species becomes available, but the exact timing of when the space becomes available combined with demographic variability among species in the local pool means that the occupation of a given microsite is largely stochastic (Chesson and Warner 1981). Because the spatial scales of such effects occur within a larger habitat comprising many microsites, the sum of which determines the local species pool of available colonists (*sensu* Zobel et al. 1998), they can be categorized as habitat scale, which is similar, though more precisely defined than the frequently used term “local scale”. In landscape ecology, it is often referred to as the scale of habitat patches (e.g. Forman and Godron 1981). Dispersal patterns are never completely random, even within a habitat patch, and it is therefore likely that the probability of colonization of any given microsite is weighted by distance and abundance of parent plants, fecundity, and dispersal mechanism. Nonetheless, local populations and communities occur at the habitat scale, as dispersal between microsites is sufficient to result in some homogeneity of composition and structure in a habitat patch.

Landscape scale

The occurrence of any particular species within a given habitat patch is often determined by the ease of immigration and colonization from other patches in the surrounding landscape (Flinn and Vellend 2005, Leibold et al. 2004). This view of habitat patches as islands is derived from MacArthur and Wilson's (1967) theory of island biogeography, and has been a critical concept in conservation biology and landscape ecology (Diamond 1975b, Turner et al. 2001). Though the definition of landscape is different for each individual species based on ecological breadth and the spatial distribution of suitable habitats, all landscapes share the common characteristic of habitat heterogeneity and spatial pattern (Turner et al. 2001). Landscape scale processes, then, operate by definition at a broader spatial scale than habitat scale processes, though the differences between microhabitat, habitat, and landscape are both subjective and species-specific. Landscape scale processes involving dispersal and colonization include disturbances that open up space and resources for colonists and maintain successional heterogeneity (Pickett and White 1985, Bullock et al. 2002), mass effects (Shmida and Wilson 1985), island biogeography (MacArthur and Wilson 1967) and metapopulation and metacommunity dynamics that link local populations and communities via dispersal (Hanski 1998, Leibold et al. 2004). The difference between populations and metapopulations (or communities and metacommunities) is a difference in dispersal; with metapopulations dispersal must be frequent enough to permit immigration, but rare enough to limit effects on local demography. The likelihood of colonization or recolonization of an empty habitat patch is dependent on distance to sources of colonists, dispersal mechanism, and the frequency and fecundity of reproductive individuals across the landscape. Even among species that frequently co-occur within a habitat, some species may be more likely to be found within the matrix

surrounding a habitat patch, thus allowing easier colonization than for species that are more spatially restricted (Murphy and Lovett-Doust 2004). Habitat isolation may also contribute to species turnover across space (beta diversity), as habitat patches that are better connected to each other across the landscape have a higher likelihood of propagule exchange and are therefore more likely to have similar local species pools (Chase 2003, Zobel et al. 1998).

Regional scale

A region can be defined as any broad, contiguous geographic area (including landscape), but boundaries between regions can be delineated in various ways, including discontinuities or steep transitions in climate, geomorphology, and floristic composition (Forman and Godron 1981, Forman 1995, Bailey 2009). Here, I define regions based on the geographic ranges of species and communities (which reflect geomorphology, climate, and geographic barriers to dispersal), so that while a landscape often includes recurring elements throughout, a region is composed of more than one landscape differing in presence or relative abundance of species and habitat types. Such a definition based on species and habitat response to climate and geomorphology is broadly congruent with the “ecoregion” concept of Bailey (2009) and with Takhtajan’s (1986) classification of floristic regions and provinces. Even regions that are relatively homogeneous in climate and geomorphology may show endemic species distributions or particular habitats restricted to only one landscape in that the sizes and locations of geographic ranges depends not only on the spatial distribution of environmental variables, but also differences between species in age, ranges of environmental tolerance and geographic barriers to dispersal. The actual spatial limits of a region are subjective because adjacent regions can be lumped together to form a broader region that shows localized species or community distributions on a scale broader than component landscapes. For example, the Great Smoky

Mountains is a landscape showing repeating units of vegetation, but the region that includes it could be the southern Appalachian Mountains, the southeastern United States in general, or all of eastern North America: each of these different scales contains endemic species and unique communities at varying levels of spatial restriction. The factors responsible for restrictions of species and communities could be differences in underlying rock type between landscapes, differences in geomorphology (e.g. mountains versus piedmont or coastal plain), or differences in climatic regime. In addition, dispersal processes may play an important role in determining the current geographic range of a species, because the relative abundance and spatial continuity of appropriate habitat varies within a region, carrying implications for spatial isolation and allopatric speciation because long-distance dispersal is rare (Brown 1984, Clark 1998, Nathan 2006, Lomolino et al. 2006). Regional scale processes therefore include speciation, climatic processes, and responses of plants to differences between landscapes in disturbance regime, geology, and topography, and correspond approximately to the Macro-scale domain of Delcourt and Delcourt (1988).

Biogeographic scale

The difference between regional and biogeographic scale is particularly difficult to assign because biogeographic processes such as migration, speciation, and extinction contribute to vegetation composition across a range of broad spatiotemporal scales (Lomolino et al. 2006). Here, I distinguish the two based on the spatial continuity of species composition, and similarity in migration histories: within a region, distribution and migration history is largely independent between species, and floristic composition may show relatively gradual spatial trends (Davis 1983, Delcourt and Delcourt 1987), whereas across two or more regions vegetation change is more abrupt and there is some indication of shared migration pathways among several taxa

colonizing a region (Forman 1995, Graham 1999). This is somewhat contingent on the spatial relationships among climatic regions, such that the boundaries between regions defined by vegetation (e.g. Braun 1950) reflect life zones with characteristic plant physiognomy (e.g. Holdridge 1967), and are ultimately explained by discontinuities in climate, often as a function of air mass boundaries (Lindsey and Sawyer 1971, Neilson et al. 1992). Historical spatial patterns of biomes and life-zones contribute substantially to explanations of floristic affinities between regions of similar climate that are currently separated. Moreover, the assembly of regional floras, and the spatial distribution of entire lineages is contingent on historical dispersal processes (Graham 1999, Manchester 1999, Donoghue and Smith 2004). A long-standing debate in the study of historical biogeography revolves around the relative importance of long-distance dispersal in creating disjunct distribution patterns among regions (Lomolino et al. 2006). The difference between vicariance biogeography, which emphasizes dispersal limitation between regions after barrier formation, and dispersal biogeography, which emphasizes long-distance dispersal events across a pre-existing barrier, is a matter of spatiotemporal scale relating dispersal curves to historical timing and arrangement of suitable habitat. Both branches emphasize the importance of dispersal (or lack thereof) in assembling regional floras, but it is likely that vicariance biogeography increases in importance with spatial scale due to increasing improbability of dispersal across extremely long distances. Although it has been shown that both long-distance dispersal and diffusive dispersal progressing stepwise across generations have been important in producing distributions of plant species within broad regions (Clark 1998), fairly abrupt differences in lineage composition between floristic regions suggests at least some similarities in colonization history among disparate taxa responding to common dispersal barriers (Tiffney 1985, Thorne 1993, Graham 1999). Dispersal between regions is a process

operating over long temporal scales, either because extreme long-distance dispersal is a stochastic and rare event, or because range expansion through diffusive dispersal must take place over multiple generations. The temporal scales of range expansion and/or long-distance dispersal can interact with the temporal scales of climate change and the formation of barriers to dispersal to produce biogeographic patterns of floristic composition across regions (Manchester 1999). Biogeographic scale corresponds approximately to the Mega-scale domain of Delcourt and Delcourt (1988), and relates to the continental and global spatial distribution of life-zones, biomes, floras, lineages, and species.

Relativity in space and time

The relative scales proposed here are based on how ecological and environmental processes interact with dispersal limitation to determine spatial pattern in distribution of multiple species of plants. It is important to reiterate that the five scales proposed here are relative, depending on the combination of species and the patterns of heterogeneity in environmental conditions affecting plants. It is therefore impractical to assign absolute ranges of space and time to each scale. Nonetheless, other systems of ecological scale classification have attempted to approximate ranges of spatial scales, and it is useful to compare the scales delineated here with other systems based on pattern or process in ecology (Table 2.1). Of note is that there is no analogue to the smallest scale of the current classification, the neighborhood scale, despite the prominent role that competition plays in ecological theory on the maintenance of diversity in plant communities (Tilman and Pacala 1993). As the differences in scales between species and systems likely show considerable variability, a process-defined system of scale classification is important to show the interaction of dispersal with environmental heterogeneity in spatial

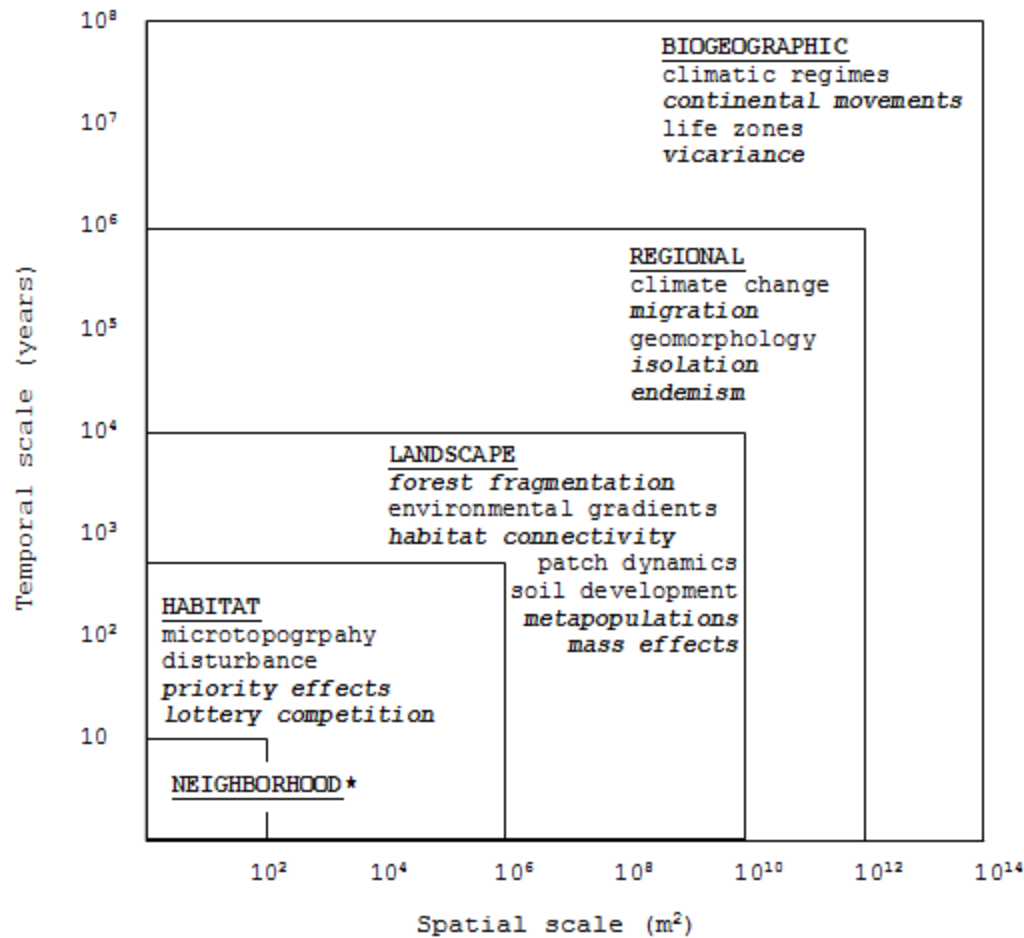
patterns of plant species diversity, and to link ecological and biogeographical processes (Figure 2.1).

Tools for assessing the importance of dispersal

Ecologists, biogeographers, and statisticians have devised several methods useful in separating the effects of dispersal limitation from more traditionally ecological processes such as niche relationships in natural patterns of diversity and species distribution. The trouble with studying dispersal, though, is that it is effectively quite difficult to obtain accurate dispersal curves (Greene and Calogeropoulos 2002), and so most studies use various proxies to infer whether dispersal processes are important in generating observed patterns. In addition, researchers often have different goals in evaluating the importance of dispersal. For example: (1) conservation biologists may focus on dispersal of individual species with the goal of either promoting or inhibiting spread at neighborhood, habitat, and landscape scales; (2) theoretical ecologists may be interested in the role of dispersal in structuring the interaction of plant species at scales ranging from neighborhood to regional scales (MacArthur 1972, Götzenberger et al. 2012); (3) community ecologists may be concerned with how landscape-scale dispersal limits community composition and species richness within a local habitat; (4) landscape ecologists may want to know the relative importance of dispersal to the spatial patterning of species composition across landscapes and regions; (5) biogeographers and ecologists concerned with climate change may study the effects of dispersal processes over long temporal scales in determining the regional distributions of plant species and lineages. Different methods of sampling and analysis are appropriate for these various goals and spatial scales.

Table 2.1. Comparison between scale classifications. Approximate spatial scales are shown in parentheses.

Current system	Delcourt and Delcourt 1988	Bailey 2009
Neighborhood scale	-	-
Habitat scale	Micro-scale ($1-10^6 \text{ m}^2$)	Site ($<10^7 \text{ m}^2$)
Landscape scale	Meso-scale (10^6-10^{10} m^2)	Landscape mosaic (10^7-10^9 m^2)
Regional scale	Macro-scale ($10^{10}-10^{12} \text{ m}^2$)	Ecoregion (10^{11} m^2)
Biogeographical scale	Mega-scale ($>10^{12} \text{ m}^2$)	Macroscale



* *seed shadows*, *intraspecific clustering*, *Janzen-Connell effects*, resource competition

Figure 2.1. Characteristic scales of environmental heterogeneity based on plant response, and associated processes affecting plant species distribution. Approximate spatial and temporal scales are based on Delcourt and Delcourt (1988). Dispersal-related processes are indicated in bold and italics.

Below, I review many possible approaches and their utility in evaluating effects of dispersal across multiple scales of spatial interaction among plants, and group methods according to the five general goals outlined above. This review is fairly comprehensive, but not exhaustive, and focuses mainly on observational methods because of the limited scope of experimental and simulation-based methods in assessing the contribution of dispersal to observed patterns of plant distribution and diversity across a broad range of scales. In addition, the subject and goals of each analysis vary from drawing inference on distributions of individual species, to co-occurrence patterns, to α - and β -diversity, to general trends among different groups of species. The strength of inference also varies among methods, where results of simulation methods are contingent on input parameters and observational methods cannot account for every possible variable. Lastly, every analysis has a different range of spatial scales to which it can appropriately be applied and for which it is practical to collect data. Therefore, I categorize methods as to subject of analysis, type of data, strength of inference, and spatial scale so as to aid in making recommendations for appropriate analyses for a range of research questions (Table 2.2). Strength of inference is entirely subjective, but is based on the type of data, how dispersal processes can be inferred, and the degree to which confounding environmental variables are likely to be included in analyses. This section makes recommendations about the appropriate analyses to use for assessing the importance of dispersal, which vary depending on the spatiotemporal scale and whether the response variable of interest is 1) individual plant species occurrence, 2) co-occurrence patterns, 3) local (α -) diversity, 4) changes in species composition across space (β -diversity), or 5) the composition of regional floras (γ -diversity).

Approaches based on dispersal of individual focal species

Quantifying autocorrelation

The only approach that actually quantifies dispersal limitation at any scale is the calculation of dispersal curves from mark-recapture methods (Jacobson and Peres-Neto 2010). With regard to plants, mark-recapture methods involve following the fate of individual seeds using stable isotopes, genetic markers, or seed traps (Clark et al. 1998b, Nathan and Muller-Landau 2000, Greene and Calogeropoulos 2002, Jacobson and Peres-Neto 2010). Unfortunately, due to the required sampling intensity, this method generally is appropriate only at neighborhood, habitat, and (rarely) landscape scales (Greene and Calogeropoulos 2002). Models of dispersal curves ('dispersal kernels') based on local data rarely fit observed patterns of regional scale migration due to underestimation of the frequency of long-distance dispersal (Cain et al. 1998, Clark 1998), but studies using landscape genetics can help identify maximum dispersal distance and quantify functional connectivity among (sub)populations (Manel et al. 2003, Manel and Holderegger 2013). One alternative to mark-recapture methods is quantifying the aggregation of individuals of a species using point-pattern analysis or autocorrelation of species abundance using spatial autocorrelation coefficients at various distance classes (Legendre and Fortin 1989, Fortin and Dale 2005). The drawback of such indirect methods is that they merely quantify spatial pattern rather than the causes of the pattern, which may result from dispersal, environmental patchiness, disturbance, or biotic interaction (Legendre and Fortin 1989, Legendre 1993). To discern dispersal processes in the midst of other processes generating spatial pattern, a simulation model may be applied that varies the contributions of several processes, and the generated patterns of aggregation or autocorrelation can be compared to observed patterns (Lin et al. 2011, Wiegand et al. 2007, 2009). If resource patches are discrete, another approach

might be to compare the aggregation of the species of interest to the aggregation of resource patches (e.g. Lancaster and Downs 2004, Belinchón et al. 2011). Mantel correlograms can portray multivariate autocorrelation in environmental conditions, so comparison of autocorrelation functions between species abundances and environmental conditions or spatial decomposition by partial Mantel correlograms may portray critical scales of endogenous autocorrelation due to dispersal limitation (with the ever-present caveat that unmeasured but spatially structured environmental variables could be driving species distributions; Legendre and Fortin 1989, Goslee and Urban 2007).

Species distribution models

Instead of quantifying dispersal limitation, habitat distribution models aim to quantify a species' response to environmental conditions. This approach is frequently used at landscape and regional scales to predict appropriate habitat (Elith et al. 2006). The same approach may be used to infer dispersal limitation from suitable but unoccupied habitats (Moore and Elmendorf 2006, Tájek et al. 2011). However, because species distribution patterns are produced both by the spatial pattern of habitat variables and by endogenous dispersal processes, an even more powerful approach is to account for spatial structure or autocorrelation within species distribution models (e.g. Keitt et al. 2002, Dormann et al. 2007, De Marco et al. 2008). One class of methods to address dispersal limitation in such models is to use a metric of habitat isolation or connectivity for each sampling point in the landscape. These metrics may be based solely on the landscape configuration of appropriate habitat or parameterized based on focal species, for instance by using an autocovariate term to incorporate occurrence or abundance in a specified neighborhood surrounding each location (Dormann et al. 2007, Dullinger et al. 2011, Tájek et al. 2011, Václavík et al. 2012). Autoregressive methods use a weighting matrix to identify

neighborhoods or levels of connectivity between sample locations, and use abundance in neighboring locations as predictors in addition to the set of environmental predictors of species abundance (Keitt et al. 2002, Lichstein et al. 2002, Dormann et al. 2007). Autogressive models can take several forms, where the simplest autoregressive (AR) model uses presence or abundance in neighboring locations as an autocovariate predicting presence in the focal location, whereas in conditional autoregressive (CAR) models the residuals from the relationship between environment and neighboring abundance are used to predict occurrence in the focal location. The primary difference in the implications of these two types of models is that in the former presence in neighboring locations is independent of environmental conditions, whereas in the later the effect of neighboring populations is contingent on the environmental conditions there. As such, CAR models are better at capturing spatial trends related to latent environmental variables, and AR models simulate spatial trends related to endogenous population processes such as dispersal (Keitt et al. 2002). Another strategy incorporates multi-scale spatial structure using spatial eigenvector mapping, a form of principle coordinates of neighbor matrices which models spatial relationships among sample locations by eigenfunction decomposition of a truncated distance matrix (Dray et al. 2006, Griffith and Peres-Neto 2006, Dormann et al. 2007, De Marco et al. 2008, Václavík et al. 2012). The product of such a strategy is a set of spatial predictor variables, each of which models spatial structure at a different scale. All methods described here can be used in the regression framework frequently employed for species distribution models, but without known absences, presence-only methods such as maximum entropy models can use only spatial eigenvector mapping or indices of habitat connectivity without regard to occurrence data unless additional variables are constructed to represent known occurrences in specified

neighborhoods (Elith et al. 2006, Phillips et al. 2006, Dormann et al 2007, De Marco et al. 2008, Václavík et al. 2012).

Landscape-scale occurrence and abundance

Natural and field experiments and observational studies often show that occurrence and abundance of particular species is limited by dispersal processes such as sources of colonists. Seed addition experiments (Vellend 2000, Turnbull et al. 2000, Clark et al. 2007), and transplant experiments (Ehrlén and Eriksson 2000) both show that occurrence and abundance in local habitat patches are limited by seed dispersal and colonization from the surrounding landscape. Observational studies also show that distance from sources of propagules is correlated with occurrence and abundance in secondary forests (Matlack 1994, Brunet and von Oheimb 1998, Takahashi and Kamitani 2004), and that measures of habitat connectivity or isolation also affect occupancy of habitat patches (Grashof-Bokdam and Geertsema 1998, Verheyen et al. 2003, Geertsema 2005). Morphological adaptations to dispersal affect rate of spread from a source of colonists and the likelihood that any given species will colonize a particular habitat patch within a broader landscape. The history and landscape configuration of habitat patches interact with dispersal mechanism to determine occurrence and abundance at habitat scales, where myrmecochorus (ant-dispersed) species and species with no dispersal adaptations are often more restricted in distribution than anemochorus (wind-dispersed), or endo- or ectozoochorous seeds (dispersed by animal eating or carrying, respectively) (Dzwonko and Loster 1992, Matlack 1994, Brunet and von Oheimb 1998, Grashof-Bokdam and Geertsema 1998, Takahashi and Kamitani 2004).

Co-occurrence based approaches

Testing hypotheses of community assembly has historically involved co-occurrence indices quantifying the non-random component of community composition at habitat and landscape scales (Diamond 1975a, Götzenberger et al. 2012). Non-random co-occurrence of species pairs is typically thought to represent deterministic processes such as competitive interactions and habitat sorting, and observed patterns of community structure or turnover are often tested against null models of community composition where species occurrences are randomized among samples across a dataset (Gotelli 2000, Gotelli and McCabe 2002, Chase and Myers 2011). In fact, one of the earliest applications of Diamond's (1975) prediction of 'checkerboard' patterns in communities as indicators of competitive processes suggested that such patterns can arise from non-spatial colonization processes alone (Conner and Simberloff 1979, Stone and Roberts 1990). Though patterns of co-occurrence in observed communities only sometimes depart from null models, non-random assemblages do not necessarily imply deterministic processes (e.g. Gotelli and McCabe 2002, Götzenberger et al. 2012), as stochastic but spatially autocorrelated dispersal processes can also lead to non-random patterns of species co-occurrence (Ulrich 2004, Bell 2005). Nonetheless, species co-occurrence patterns can be useful for discerning the importance of dispersal from deterministic processes under particular conditions. At the habitat scale for instance, if multiple sampling locations share a local species pool, dispersal limitation can be assumed to be minimal, so competitive interactions can be inferred to generate non-random patterns. At landscape scales however, habitats are similar and the regional species pool is shared between sample locations, but non-random patterns can be caused by dispersal limitation between habitat patches or demographic stochasticity (Hanski 1996, Zobel et al. 1998). Of course, assumptions of minimal dispersal limitation or habitat

similarity are subjective, but comparison of departures from random patterns across scales may suggest some structuring processes (Jenkins 2006, Chase et al. 2011). A more powerful method for differentiation between niche and spatial drivers of non-random co-occurrence patterns may be in the comparison between completely randomized null models and null models that only randomize species occurrences in localized neighborhoods or in habitat types, thereby retaining either spatial autocorrelation or habitat constraints in the null model (Watkins and Wilson 1992, Peres-Neto et al. 2001, Cornell et al. 2007). Investigation of co-occurrence patterns of individual pairs of species might be more meaningful than whether co-occurrence of an entire community is non-random, as only a few non-randomly co-occurring pairs among all possible combinations may indicate non-random structure for the community at large (Silvertown and Wilson 1994, Livingston and Philpott 2010). Such an approach might be especially useful in differentiating co-occurrences across scales, as a pair of species may show, for instance, overdispersion at a neighborhood scale due to competition or localized dispersal, aggregation at a habitat scale due to similar or spatially correlated environmental conditions, random relationships at a landscape scale due to metapopulation dynamics, stochastic dispersal, and individualistic responses to environmental conditions, and overdispersion at regional scales due to separate ranges and migration histories.

Approaches addressing the effects of dispersal and colonization on α -diversity

Local diversity, or α -diversity, has no absolute spatial scale, but is generally understood to be measured at habitat scales (Whittaker 1972, Ricklefs 1987). α -diversity is usually documented by either species richness or an index that combines species richness with relative abundance (Peet 1974, Magurran 2004). Though often associated with niche processes that constrain the number and identity of locally co-occurring species, α -diversity is limited by

broader scale colonization processes (Ricklefs 1987, Myers and Harms 2009). One approach to assessing the effects of dispersal and colonization on local diversity is to test for saturation (*sensu* Cornell and Lawton 1992) of the local species pool using seed addition experiments in natural communities (Cadotte 2006, Myers and Harms 2009). The same approach is often applied at the population level to investigate whether the presence, absence, or abundance of particular species is limited by dispersal and colonization processes (e.g. Turnbull et al. 2000, Clark et al. 2007). An observational approach to correlations between dispersal processes and local diversity is another common strategy. Some studies compare species richness between habitat patches of different ages, and frequently find that more recent habitat patches have a reduced richness, presumably owing to temporal scale and the reduced frequency of landscape scale dispersal compared to habitat-scale dispersal (Peterken and Game 1984, Bellemare et al. 2002). Others look at distance from sources of colonists (also habitats of older age) as a predictor of species richness and composition (Dzwonko and Loster 1992, Matlack 1994, Brunet and von Oheimb 1998, Takahashi and Kamitani 2004). Measures of habitat connectivity or isolation are also influenced by distance from sources, but frequently show further impact on species richness and composition due to difficulties in dispersal across unsuitable habitats (Peterken and Game 1984, Matlack 1994, Hérault and Honnay 2005). Local species composition in young or isolated habitat patches may be particularly impacted by differential dispersal probabilities among plant species, and is often shown to be depauperate in species without morphological adaptations to long distance dispersal (e.g. seeds dispersed ballistically from fruits only short distances, myrmecochorous seeds, and plants without morphological dispersal adaptations; Dzwonko and Loster 1992, Matlack 1994, Bellemare et al. 2002, Takahashi and Kamitanti 2004, Hérault and Honnay 2005).

Approaches analyzing or explaining β -diversity

The many approaches described above address the questions of *whether* or *how* dispersal processes affect plant species occurrence, abundance, and community composition, but, in order to distinguish spatial autocorrelation caused by dispersal from environmental variation, both of which can affect spatial pattern, analyses of how community composition changes across space (β -diversity) are required to quantify the *relative importance* of dispersal processes compared to environmental determinism. With the emergence of neutral theory, the appreciation that natural systems have both deterministic and stochastic elements, and the increasing recognition of the importance of linking processes across multiple scales, studies involving β -diversity have increased in popularity as a way of linking local and regional processes (Hubbell 2001, Ricklefs 2004, Anderson et al. 2011). The reason for this is somewhat intuitive, given that β -diversity by definition links local (α) and regional (γ) diversity, but implies that local and regional processes are mutually exclusive with respect to scale rather than relative (Whittaker 1972). Regardless of variation in spatial scale and the multitude of measures of β -diversity, however, the concept is useful because it allows ecological phenomena to be placed in a spatially explicit framework (Tuomisto 2010a,b, Anderson et al. 2011). Although dispersal processes cannot be realistically measured explicitly for all species across a broad range of scales, spatial relationships are used as a proxy in the two main methods frequently used to differentiate the relative importance of environmental and niche-based phenomena and spatial dispersal-based phenomena. The two methods differ both in broad definitions of beta-diversity and in statistical decomposition of variation, and though the second method is currently thought to be the most powerful, is it also more difficult to interpret ecologically, so that a holistic understanding of spatial and ecological processes may be best achieved by using both approaches (Tuomisto and Ruokulainen 2006,

Legendre et al. 2005, 2008). Both approaches address the question of how much changes in community composition across space are related to changes in environmental conditions versus purely spatial autocorrelation, and are best applied at landscape and regional scales. Either approach can be adapted to include variables for habitat connectivity as a representation of dispersal limitation in addition to spatial relationships (e.g. Griffith and Peres-Neto 2006, Minor et al. 2010).

Distance approach

The oldest and simplest approach to differentiating spatial autocorrelation in plant community composition from environmental heterogeneity is based on distance or (dis)similarity matrices (Legendre and Fortin 1989, Legendre 1993). The method is conceptually allied with the trend of distance decay of similarity, or the tendency of pairwise measures of community similarity to decrease with increasing spatial distance (Nekola and White 1994, Morlon et al. 2008). A matrix of pairwise (dis)similarity in species composition across sample locations is correlated with a matrix of pairwise (dis)similarity of environmental locations and a geographic (Euclidean) distance matrix. Because spatial autocorrelation in species composition can be caused either by endogenous (dispersal) processes or spatially correlated environmental conditions, a partial Mantel test controls for the tendency of nearby sites to be more environmentally similar by performing a partial correlation that accounts for the correlation between the two predictor matrices (Mantel 1967, Smouse 1986). Because the assumption of independence in parametric tests is violated by distance matrices, the significance of the Mantel statistic is tested by permutation (Legendre and Legendre 1998). Any measure of distance may be used in Mantel tests, however the test is subject to the same assumption of linearity as the Pearson correlation, so variation resulting from nonlinearity in the relationship between distance

matrices may be left unexplained (Legendre and Legendre 1998). Although Mantel tests say nothing about the scales of multivariate autocorrelation, various modifications including the Mantel correlogram provide ways of portraying multivariate spatial autocorrelation at various scales, and may be used to investigate spatial structure of ecological communities. Traditionally, the Mantel correlogram is calculated by correlating a matrix of multivariate (dis)similarity among sampling locations with a series of binary matrices specifying membership in a particular distance class, and can be interpreted similarly to univariate correlograms using Moran's I or Geary's c (Legendre and Fortin 1989, Fortin and Dale 2005). A modification of Mantel correlograms can additionally allow for correlations between distance matrices at different lag distances (Goslee and Urban 2007). Also, multiple regression on distance matrices, an extension of partial Mantel tests, allows the statistical flexibility to account for nonlinearities (Lichstein 2007). The distinguishing characteristic of all distance-based approaches is that the response variable is pairwise (dis)similarity in community composition (a measure of β -diversity), so that in contrast to the constrained ordination approach (described below), these tests ask how much variation in β -diversity is explained by variation in spatial distance versus variation in environmental differences (Tuomisto and Ruokolainen 2006).

Constrained ordination approach

The question of interest in the constrained ordination approach to variation partitioning is how much variation in community composition can be explained by variation in environmental conditions versus variation in spatial relationships. The dependent variable is community composition, so that β -diversity is the output rather than the input in such analyses (Tuomisto and Ruokolainen 2006, Legendre et al. 2008). This method is performed using partial canonical ordination techniques on data matrices giving sampling site by variable combinations, where the

dependent matrix is formatted as sampling site by species and the predictor matrices are site by environmental variable and site by spatial variable combinations. Canonical ordinations are methods of constrained ordination where sampling points are first regressed on a matrix of predictor variables, and then ordinated by either by correspondence analysis (in the case of canonical correspondence analysis) or by principal components analysis (in the case of redundancy analysis; Legendre and Legendre 1998). In using partial canonical ordination for variance partitioning, two (or more) matrices of predictor variables are used to constrain ordinations of the species matrix separately, partially, and combined to test the partial variation explained by each matrix as well as their common effect. While one predictor matrix contains data for various environmental variables at each site, the spatial predictor matrix contains variables for the geographic locations of each site, a polynomial function of their geographic locations, or dummy variables that model spatial relationships between sampling locations produced using a method such as principal coordinates of neighbor matrices (PCNM; Borcard et al. 1992, 2004, Borcard and Legendre 2002). PCNM models spatial relationships across multiple spatial scales by eigenanalysis of a truncated spatial distance matrix (principal coordinates analysis), where distances beyond a chosen neighborhood threshold are designated as arbitrarily long (Borcard and Legendre 2002, Borcard et al. 2004, Dray et al. 2006). Though it is easy to understand how the probability of dispersal between locations relates to their distance apart (as in the distance approach, above), it is not quite so intuitive how dispersal processes might be represented by PCNM eigenvectors, however the PCNM approach to variation partitioning has the interpretability advantage that community composition in any one location can be influenced by local environmental variables as well as its spatial relationships to *multiple* other sampling locations (Borcard et al. 2004).

Approaches assessing the influence of dispersal processes on regional (gamma) diversity

The composition and diversity of regional floras emerges from the spatial distributions of the ranges of component species. Ranges of species can be defined in two main ways: the spatial extent or area of occupancy within the broader area delimited by the outermost limits of species occurrence (Gaston 1996). There are a number of reasons to expect dispersal processes to contribute to both range extent and frequency: 1) if range is defined by frequency of occurrence across space, and frequency is influenced by dispersal from local populations, then range is linked to local abundance through metapopulation dynamics (Hanski 1982); 2) local abundance is generally positively related to both range extent and frequency (Hanski 1982, Brown 1984); 3) rare, long-distance dispersal events account for rapid migration and range expansion from glacial refugia (Cain et al. 1998, Clark et al. 1998a); 4) potential and realized ranges differ for many plant species, in many cases owing to postglacial migrational lag (e.g. Svenning and Skov 2004, 2007); and 5) occurrence of species in any region is contingent on the historical dispersal processes of ancestral lineages (Manchester 1999, Xiang and Soltis 2001, Donoghue and Smith 2004, Lomolino et al. 2006). Approaches that build on those processes described in sections above, correlative approaches appropriate across a range of scales, and novel approaches applicable only at regional and biogeographic scales are available for evaluating the role of dispersal in assembling regional floras. Here I categorize approaches into 1) methods addressing plant migration, 2) comparative and correlative approaches, and 3) phylogeographic inference and analyses.

Plant migration

Glaciation in the Northern Hemisphere has had dramatic consequences for the current distributions of plant species, as climate changes in the Pleistocene changed the abundance and

configuration of appropriate habitat for many species, often restricting ranges during glacial maxima to small refugia (Davis 1983, Jackson et al. 2000, Soltis et al. 2006). Though exact locations of refugia are can only be hypothesized based on pollen records, genetic variation, and current plant species distributions (Delcourt and Delcourt 1975, 1987, Davis 1983, Jackson et al. 2000, Soltis et al. 2006), the history of dispersal and colonization processes from these refugia can be inferred by modeling past climates, current habitat distribution, or dispersal processes for various taxa. Given what we now know of the history of Quaternary climate changes (e.g. Delcourt and Delcourt 1987, Jackson et al. 2000), it is recognized as quite anomalous that many plant species have recolonized much farther north than would be predicted from the amount of time since glacial retreat and the typical dispersal distances of plant species; this suggests that long distance dispersal by atypical means has played a disproportionate role in postglacial colonization (Cain et al. 1998, Clark 1998, Clark et al. 1998a). Though some plant species may be near to equilibrium with current climate (e.g. Webb 1986), it can be shown using species distribution modeling that the potential ranges of many species differ from their actual ranges (Svenning and Skov 2004, Svenning et al. 2008a), and that models including variables for accessibility to refugial areas are better predictors of most species occurrences than those including only habitat variables (Svenning et al. 2008b, Normand et al. 2011). Furthermore, accessibility from hypothesized glacial refugia may be a stronger predictor than climate for patterns species richness (Svenning and Skov 2007).

Comparative and correlative approaches to species distributions

Comparison of β -diversity among organisms and within and among regions and may highlight trends related to dispersal processes. Because frequency of occurrence across geographic ranges is intuitively related to β -diversity (where plants of high frequency show

lower spatial variation; Morlon et al. 2008), comparison among organisms may show that groups of species with shorter average dispersal distances have higher regional β -diversity (Nekola and White 1999, Soininen et al. 2007, Qian 2009). Trends in β -diversity may also be related to geography, as higher β -diversity is often found at lower latitudes in temperate zones (also longitudinal trends varying by region), suggesting that after accounting for climate, postglacial dispersal limitation can explain regional trends (Soininen et al. 2007, Qian et al. 2005, Qian and Ricklefs 2007, Qian 2009).

Comparison of patterns of species diversity to those predicted by various models of community interaction is another commonly used method to discern dispersal-based processes (i.e. neutral models) at habitat, landscape, and regional scales (Hubbell 2001, Chave et al. 2002, McGill et al. 2006). Examples include comparing species abundance distributions, species-area curves, and distance-decay relationships to patterns predicted or generated by various combinations of niche and neutral processes in homogeneous and heterogeneous landscapes (Chave and Leigh 2002, Chave et al. 2002, Wang et al. 2011). These methods are more qualitative than quantitative, and incorporate α , β , and γ diversities, but highlight composite patterns resulting from the dynamics of multiple species in a region.

Because there are theoretical reasons to expect both current and historical dispersal processes to have affected range extent and frequency (see above), a set of interrelated approaches relating dispersal, range size, frequency, and biogeographic affinity can give insight into the effects of spatial and temporal dispersal processes on γ -diversity. First, correlating dispersal distance or morphology to range extent may elucidate whether local and/or long-distance dispersal influence range size, though many other processes affect range extent in addition to dispersal (Oakwood et al. 1993, Lavergne et al. 2004, Lester et al. 2007). Second,

range occupancy may reveal the importance of dispersal processes if dispersal-limited species are more infrequent across the landscape or region (Matlack 2005, Ozinga et al. 2005, Gove et al. 2009), and may influence regional persistence (Soons and Ozinga 2005). Third, because the positive relationship between local abundance and range occupancy can be generated by colonization and extinction dynamics between local populations, which predicts a bimodal frequency distribution of range occupancy (core-satellite hypothesis, Hanski 1982), assessment of which dispersal groups have bimodal distributions can indicate whether dispersal processes play a major role in structuring range-wide occurrences (Collins and Glenn 1991, Mehranvar and Jackson 2001, Murphy et al. 2006). Finally, because geographic ranges of entire lineages are affected by dispersal and vicariance (see below), examination of the relationships between biogeographic affinity, current range, and traits including dispersal morphology may give insight into the role of dispersal in assembling regional floras (White 1983, Weakley 2005).

Phylogeographic inference and analyses

Elucidating the effects of historical dispersal processes on the composition of regional floras involves reconstructing the colonization and distributions of various lineages of plants through time. Phylogeographic methods for revealing spatial and temporal trends of lineage distribution rely on detailed phylogenetic relationships of taxa and estimations of the timing of divergence among species and clades (Lomolino et al. 2006). Some methods are comparative among taxa and rely on comparing current distributions of plant taxa to show spatial and temporal patterns of vicariance using general area cladograms (Arbogast and Kenagy 2001, Donoghue and Moore 2003). Others are more quantitative and can resolve patterns derived from vicariance versus those generated by long-distance dispersal (van Veller et al. 2003). Though the biogeographical view of vicariance and dispersal is dichotomous and "dispersal" processes often

have an unresolved spatial scale (Arbogast and Kenagy 2001, Lomolino et al. 2006), modern analytical methods can still illuminate complicated patterns within and among taxa regarding differences between clades in divergence times and the relative frequency of dispersal, vicariance, and extinction events (Xiang and Soltis 2001, Donoghue and Moore 2003). Among these, Brooks Parsimony Analysis (BPA) and phylogenetic analysis for comparing trees (PACT) generate general area cladograms to show vicariance relationships and incongruences caused by long-distance dispersal among taxa (van Veller et al. 2003, Wojcicki and Brooks 2005), while dispersal-vicariance analysis (DIVA) uses cost weighting to globally optimize a model to generate a probable history of vicariance and dispersal events (Ronquist 1997, Lomolino et al. 2006). The use of geological and fossil evidence can provide additional data for comparison to results predicted by phylogeographic analyses and can suggest a geographic context for convergent or divergent histories among taxa with varying dispersal abilities (Tiffney and Manchester 2001, Donoghue and Smith 2004). In addition to analysis of individual clades, Graham and Fine (2008) propose using a metric of phylogenetic beta diversity to analyze differences in phylogenetic composition between areas compared to be what would be predicted under different combinations of environmental conditions and measures of geographic isolation or historical connectivity. This approach could be used similarly to the distance approach to beta diversity as described above, but could be applied at biogeographic scales.

Summary, synthesis, and conclusion

Ecologists and biogeographers are constantly faced with dilemmas of data collection: the strongest inferences as far as cause and effect in science always emerge from experiments in controlled conditions, yet real ecological interactions are so multivariate that it often becomes impossible to control every variable. Studies simulating effects of limited dispersal indicate that

dispersal is potentially an important process structuring biodiversity (e.g. Hubbell 2001, Chave and Leigh 2002). However, the closest we can get to quantifying what is *actually* controlling plant species distribution and diversity, rather than what factors could *possibly* influence patterns, is to use field and natural experiments. With field experiments such as seed addition and transplants, we can fairly confidently address *whether* dispersal is limiting to diversity or distribution, but inference can be drawn mostly at site-specific habitat scales. Natural experiments are better at addressing questions of *how* dispersal processes are affecting composition and distribution, for instance by using mark-recapture or distance from sources of propagules to measure dispersal (e.g. Peterken and Game 1984, Matlack 1994, Clark et al. 1998b, Takahashi and Kamitani 2004). The strength of inference is also fairly good in these methods, though they are practical only at habitat and small landscape scales. Use of genetic markers can broaden the scope to landscape or regional scales, but also adds the expense of analyzing genetic material, is complicated by the fact that the spatial distribution of plant genetics is determined both by seed and pollen dispersal (of course, pollen often travels much farther than seeds), and is generally only reliable if multiple markers are used (Ouborg et al. 1999). Landscape genetic approaches are recommended for studies of how populations and metapopulations are spatially structured due to the spatial distribution of appropriate habitat and dispersal limitation. Observational studies have a relatively broad scope in terms of applicable scales, and have the advantage that data collection is relatively easy. They are also far more likely than experimental or simulation methods to address questions of how dispersal processes operate to structure natural distributions and communities in the presence of several interacting ecological processes, though this comes at the expense of strength of inference, which is weaker when all variables cannot be controlled or even accounted for and when dispersal cannot be

measured directly. Nonetheless, observational methods are the focus of this review because of their broad range of scales and applicability to multiple systems, subjects, and datasets. While it is often difficult to discern causative factors in studies that don't measure environmental variables or dispersal directly (e.g. point pattern, comparative and macroecological studies), studies such as these excel in revealing trends across a range of spatial scales and can advise decisions on future analyses. Observational methods that can differentiate among causal mechanisms, such as species distribution models, Mantel tests, and variation partitioning, stand out particularly because they can incorporate both environmental variables and spatial relationships, and make it possible to estimate the relative importance of dispersal processes across a range of subjects and spatial scales. The strength of inference is relatively strong in these studies, despite the fact that dispersal cannot be measured directly.

Clearly, plant dispersal is a complicated subject of study due to difficulties in direct measurement, interaction with spatial patterns of environmental variables, and spatial and temporal scale dependence. Yet understanding the implications of dispersal processes across spatial scales is integral to uniting ecology and biogeography. It is important to recognize that different researchers have different questions with regard to the implications of dispersal processes depending on their study subject, system, spatial scale, and that there is no one method of analysis that can be recommended for all questions about how dispersal processes affect the distribution and diversity of plant species. Table 2.2 therefore provides a guide for researchers to choose a spatial scale of interest, and summarizes several methods and associated advantages and disadvantages for their particular study subject, system, and scale.

Plant dispersal is a process that operates across multiple spatial scales, and the dynamics of dispersal vary across space and time and among taxa. The ecological and biogeographical

consequences of dispersal depend on a taxon-specific dispersal curve, the spatial and temporal configuration of appropriate habitat, and ecological and life-history parameters that affect colonization probability (e.g. morphological dispersal adaptations, fecundity, dormancy, and frequency). Dispersal and ecological interaction are not mutually exclusive processes, but affect each other differently depending on spatiotemporal scale. Depending on the questions and goals of individual researchers, many methods are available to assess the importance of dispersal to plant species occurrence, distribution, diversity, range, and floristic composition. Some methods target individual species, others evaluate α -, β -, or γ -diversity, and though explicitly quantifying dispersal is mostly realistic only at the level of individual species and at narrow scales, various spatial proxies allow us to infer that dispersal is important across multiple scales. Development of additional approaches may allow us to more accurately quantify dispersal curves and to investigate scalar trends in the relative importance of dispersal in the context of ecological and evolutionary interactions.

In the following three chapters, I use some of the approaches described above to assess the importance of dispersal at habitat, landscape, regional, and biogeographical scales for the flora of mixed mesophytic forests of the southern Appalachian Mountains. Chapter 3 uses approaches for individual species in quantifying autocorrelation and incorporating spatial pattern into species distribution modelling; Chapter 4 analyzes nonrandom co-occurrence patterns and β -diversity in relation to spatial and dispersal processes; and Chapter 5 uses correlative approaches to relate dispersal mechanism to geographic range, landscape-scale occupancy, and biogeographic affinity. Together, these three chapters show the importance of dispersal to the mixed-mesophytic flora across several levels of biotic organization and multiple spatial scales.

Table 2.2. Approaches to evaluating effects of dispersal on plant diversity and distribution. The approaches discussed are contrasted in terms of subject (dependent variable), which proxy (if any) is used for dispersal, if/how environmental variables are included in analysis, the strength of inference, the nature of the data, and recommended applicable scales.

<i>Approach</i>	<i>Subject</i>	<i>Dispersal measurement</i>	<i>Environment</i>	<i>Inference</i>	<i>Data type</i>	<i>Appropriate scales</i>
<i>Mark recapture</i>	population	direct	n/a	strong	experiment	neighborhood, habitat
<i>Genetic markers</i>	population, species	direct	n/a	medium	experiment	landscape
<i>Point pattern</i>	population	spatial	none	weak	observation	neighborhood, habitat
<i>Simulated pattern</i>	population, alpha, beta diversity	simulation	simulation	medium	observation, simulation	neighborhood, habitat, landscape
<i>Mantel corellogram</i>	population, species, beta diversity	spatial	measured	medium	observation	neighborhood, habitat, landscape, region
<i>Species distribution model</i>	species	spatial, connectivity	measured	medium	observation	landscape, region
<i>Saturation/transplant</i>	species, alpha diversity	experimental	constant	strong	experiment	habitat
<i>Landscape occurrence /abundance</i>	species, alpha diversity	morphology, distance	assumed constant	medium-strong	natural experiment	landscape
<i>Co-occurrence</i>	co-occurrence	spatial separation	n/a	weak	observation, simulation	landscape
<i>Variance partitioning</i>	species, community composition	spatial	measured	medium	observation	neighborhood, habitat, landscape, region
<i>Distance</i>	beta diversity	spatial distance	measured	medium	observation	neighborhood, habitat, landscape, region
<i>Plant migration</i>	species	simulation, distance to refugia	measured	medium	observation, simulation	regional, biogeographic
<i>Beta diversity comparison</i>	beta diversity	morphology	n/a	weak	observation	landscape, region, biogeographic
<i>Macroecology</i>	dispersal morphology	morphology	n/a	weak	observation	landscape, region, biogeographic
<i>Phylogeography</i>	lineage	divergences	n/a	medium	observation, simulation	biogeographic
<i>Phylogenetic beta diversity</i>	phylogenetic beta diversity	historic connectivity	can be measured	medium	observation	regional, biogeographic

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CHAPTER 3. DISCERNING SPATIAL AUTOCORRELATION FROM SPATIAL DEPENDENCE IN PLANT SPECIES DISTRIBUTION MODELLING

Introduction

One of the major limitations to understanding and predicting species distributions is the extent to which spatial processes such as dispersal and habitat connectivity affect local occurrences. Modelling of species distributions typically relies only on environmental and habitat variables in order to model niche relationships of particular species (Soberón and Peterson 2005, Elith and Leathwick 2009, Boulangeat et al. 2012). Few models incorporate spatial processes such as distance-dependent dispersal or habitat connectivity, assuming that species are in equilibrium with their environment, but there are several ways to incorporate spatial dependence and autocorrelation into models that can better predict realized distributions (Austin 2002, Dormann et al. 2007). Spatial predictors are most often applied to species distribution models for animals, as plants are sessile and therefore strongly dependent on their local environment (Guisan and Thuiller 2005, Miller et al. 2007, Elith and Leathwick 2009). Despite this, as passive dispersers, plants are often more dispersal-limited than animals, so incorporation of spatial patterns may both improve the predictive power of models and indicate the extent to which plant species distributions are restricted by dispersal processes (Kinlan and Gaines 2003, Elith and Leathwick 2009).

One way to incorporate spatial or dispersal processes into species distribution models is to use indices of habitat connectivity as spatial predictors, under the assumption that it is more

difficult for many species to spread across unsuitable habitat (Murphy and Lovett-Doust 2004, Dray et al. 2006, Griffith and Peres-Neto 2006). The effects of habitat connectivity on plant dispersal have most often been studied in the context of fragmented landscapes (Pearson et al. 1998, Flinn et al. 2005), but it is reasonable to extend this logic to natural landscapes if habitat patches are fairly discrete (e.g. Demars and Harper 2005). Other methods use models of multiple scales of spatial relationships as additional predictors, regardless of whether spatial relationships may be due to spatial autocorrelation or the spatial dependence of environmental variables (Borcard and Legendre 2002, Dray et al. 2006, Griffith and Peres-Neto 2006). Explicitly incorporating response in nearby or connected locations as a predictor, as in autocovariate or autoregressive methods, is perhaps the most intuitive way of accounting for autocorrelation in cases where dispersal processes are suspected of affecting species distribution (Augustin et al. 1996, Keitt et al. 2002, Lichstein et al. 2002, Dormann et al. 2007). Each of these methods can augment niche models by adding extra predictors to represent connectivity, spatial pattern, or responses in nearby locations, and comparison between spatial and non-spatial models can assess the importance of spatial pattern and autocorrelation on species distributions (Legendre 1993, Fortin and Dale 2005, Dormann et al. 2007). Inclusion of spatial predictors not only reflects endogenous processes such as dispersal, but also spatially correlated environmental variables, such that parameter estimates for environmental variables can shift significantly between spatial and non-spatial models, and models that include only spatial predictors can actually outperform models with only environmental predictors (Lichstein et al 2002, Bahn and McGill 2007, Bini et al. 2009). The importance of dispersal and connectivity in the context of spatial dependence on environmental conditions in plant species distributions is thus best assessed through comparisons of total predictive power between spatial and non-spatial models.

Here I use two classes of models to assess the influence of spatial and dispersal processes on plant species distribution in coves and mesophytic habitats of the Great Smoky Mountains National Park (GRSM). Dispersal processes are addressed both through comparison between categories of plant dispersal morphology and between spatial and non-spatial models incorporating spatial relationships and habitat connectivity. Though several methods of incorporating spatial phenomena into species distribution models have been proposed, I use two methods as examples of how model performance can differ based on dispersal mechanism, scale, and how spatial processes are incorporated. The relative performance of these models can thus be used as an indicator of which species and scales are most strongly influenced by spatial processes and local environmental conditions. First, I use maximum entropy models with additional variables representing spatial pattern (spatial eigenvector mapping) and categorical habitat connectivity (Dray et al. 2006, Griffith and Peres-Neto 2006, Phillips et al. 2006). I also use logistic regression with an additional autocovariate weighted by spatial distance and habitat connectivity classes to predict occurrence based on both local environmental variables and presence in nearby or connected locations (Augustin et al. 1996, Dormann et al. 2007). Because many species are dispersal limited at broad scales and spatially clumped at narrow scales (due to dispersal limitation or vegetative growth), and because presence/absence data better reflect dispersal processes than abundance data (Addicott et al. 1987, Boulangeat et al. 2012), I use occurrence data collected at three nested spatial scales across GRSM to test the hypotheses that 1) inclusion of spatial pattern and habitat connectivity increases predictive power of species distribution models, 2) models based on purely environmental variables should be more accurate for species with morphological adaptations to long distance dispersal, whereas models that also incorporate spatial pattern will have a stronger relative performance for dispersal limited species,

and 3) differences between spatial and non-spatial models should be smallest at intermediate sampling scales, as many species are clumped at neighborhood scales and dispersal limited at landscape scales.

Methods

Vegetation

Mesophytic habitats are among the most floristically diverse areas of the southern Appalachian Mountains, and are home to a diverse array of plant species, many of which are restricted in distribution to nutrient-rich coves predominantly distributed around stream drainages, but are also affected by underlying geology. An advantage of sampling a well-studied natural landscape such as that of GRSM is that it is easy to target potential sampling areas at several levels of habitat connectivity using a vegetation map of the park, which maps major community types in the park based on remote sensing data combined with elevation, topographic position, and vegetation field data (Madden et al. 2004). I stratified sampling across the park so as to capture several vegetation samples in 1) the same habitat patch, and 2) separate but nearby habitat patches connected by marginally appropriate mesic habitat. In addition, because mesophytic areas are located predominantly along stream drainages, I used three additional connectivity levels based on stream, small river, and large river watersheds, each of which indicates current or historical corridors of similar habitat. Overall, 47 hectare plots were laid out across the park, and all vascular plant species were recorded in each hectare, adding up to a total of 396 species. Within each hectare plot, two 20 by 50 meter plots were sampled intensively for all vascular plant species, each of which contained four 10 by 10 meter modules, within each of which all vascular plant species were identified and recorded. This yielded three nested sampling scales, an approach modified from the Carolina Vegetation Survey Protocol (but without nested

corners; Peet et al. 1998). For this study, I selected species for modelling that were present in at least 25% but less than 65% of all hectares, because species that are either too common or too rare in the dataset generate models with poor fit (Elith et al. 2006) resulting in 93 species modelled. I analyzed data from two of the four intensively sampled modules in each plot, corresponding to the locations from which soil samples were collected (see below). Each species' dispersal syndrome was assigned based on seed, fruit, or spore morphology as described by van der Pijl 1969 (Appendix 2), and grouped into categories representing wind dispersal (seeds/fruits with winged or plumed appendages, plants dispersing by spores, and plants with <0.5 mm seeds), vertebrate dispersal (endozoochory, epizoochory, and dyszoochory), and local dispersal (myrmecochory, autochory, and barochory).

Environmental variables

Soil samples were collected in the top 10 centimeters of each intensively sampled module and analyzed for extractable micro- and macronutrients using a Mehlich III extraction technique (Mehlich 1984) by Brookside Labs, New Bremen, Ohio. In addition, several variables were extracted for each sample unit using ArcGIS 10.3, including soil mapping unit, dominant series, subgroup, and order (USDA 2009); bedrock formation, group, and surficial deposits (Southworth et al. 2012); disturbance history (Pyle 1985); elevation, slope, and aspect (NPS 2011); topographic indices of soil moisture (NPS 2013, 2014); and temperature parameters (Fridley 2011). All variables were extracted within a 10-m buffer zone of the edges of each sample unit. Aspect was first transformed to continuous unidirectional variables (Beers et al. 1966, Clark et al. 1999), then each of the continuous variables were averaged for each sample unit. To account for topographic heterogeneity, variance in Beers aspect was also calculated (Beers et al. 1966).

For regression, categorical variables (soil type, geology, and disturbance) were transformed to dummy variables.

Spatial modelling

Additional variables representing spatial pattern can be generated for incorporation into species distribution models through Moran's eigenvector mapping (MEM), a modified form of principal coordinates of neighbor matrices (PCNM), which models potential spatial pattern at multiple scales based on the locations of sample units. The process works by eigenfunction decomposition of a (weighted) truncated distance matrix, where the truncation distance designates sites far enough apart that they cannot be considered neighbors (Borcard and Legendre 2002, Dray et al. 2006, Griffith and Peres-Neto 2006). In the case of MEM, eigenvectors represent spatial pattern in the data if they maximize Moran's I index of autocorrelation (Dray et al. 2006). To model spatial relationships in my dataset, I used a truncation distance t for each sampling scale corresponding to the maximum distance in the minimum spanning tree that connects all sampling sites, and weighted the neighbor distance with the inverse square of $4t$, as suggested by Dray et al. 2006 and Griffith and Peres-Neto 2006. I selected only the spatial eigenvectors corresponding to positive eigenvalues that minimize spatial autocorrelation of the residuals of a generalized linear model, and included these as predictor variables in maximum entropy (MaxEnt) modelling (Phillips et al. 2006). In addition to the selected spatial eigenvectors for MaxEnt models, I used environmental variables as well as categorical dummy variables representing habitat connectivity levels as described above. To construct an autocovariate for logistic regression (logit) models, I used a weighting matrix constructed by multiplying connectivity weights (1 for large river, 2 for small river, 3 for stream, 4 for network, and 5 for patch) by the inverse Euclidean distance among sample locations,

thereby allowing nearby locations with higher degrees of habitat connectivity to more strongly influence results. For each sample location then, the weighted average of species presences in all other (connected) locations becomes the autocovariate (Augustin et al. 1996, Dormann et al. 2007).

Statistical analysis

Autocorrelation of species and individual environmental variables were quantified at a range of lag distances using Moran's *I* coefficient of autocorrelation, tested by randomization. In addition, multivariate spatial autocorrelation of environmental conditions was calculated using Mantel's *R* statistic for correlation between matrices representing environmental dissimilarity (Mahalanobis distance) and distance class membership between sample locations. Both statistics range from -1 for perfect negative autocorrelation to 1 for perfect positive autocorrelation (Legendre and Legendre 1998, Fortin and Dale 2005, Bivand et al. 2008). For each species and each spatial scale as described above, species distribution models were trained with a random subset of data from half of all sample locations. This allowed me to test the predictive power of the two types of models using both presence and absence data despite the fact that MaxEnt requires only presence data to construct species distribution models, and therefore internally evaluates model performance based only on "pseudo-absences" (Phillips et al. 2006). Because the same random subset was used to train both the MaxEnt and logistic regression models, it is possible to evaluate differences in performance directly between spatial and non-spatial models, and between the two different statistical methods and how they can incorporate spatial data. To add Moran eigenvectors to MaxEnt, I first used permutation-based forward selection to identify the important environmental variables affecting each species distribution, then used those selected variables to extract the spatial eigenvectors that document spatial pattern in the species

data not explained by spatially dependent environmental variables. I then ran MaxEnt twice, first using only environmental data, then adding both the selected spatial eigenvectors and the five variables representing levels of habitat connectivity. I used stepwise model selection to select environmental variables for logistic regression, and created two generalized linear models based on 1) only those variables selected, and 2) the same variables plus the autocovariate. To evaluate model performance, I calculated the area under Receiver Operating Characteristic curves (AUC), which measures the relationships between true positives and false positives predicted by the models. AUC can range from 0 to 1, where 1 indicates perfect discrimination between predicted presence and absences, 0.5 indicates a model that performs only as well as random assignment of presences and absences among samples, and less than 0.5 indicates a model that does worse than random assignment, which can happen if model training data do not reflect test data (Hanley and McNeil 1982, Elith et al. 2006). AUC was calculated for each species, model, and spatial scale. The Wilcoxon signed-rank (positive) V test statistic was used to test for (paired) AUC differences between spatial and non-spatial models and between spatial scales, and Kruskal-Wallis rank sum tests were used to compare AUC between broad dispersal categories. All data manipulation, modelling and statistical analyses were performed using R (R Core Team 2016) with the packages 'dismo', 'ecodist', 'packfor', 'pgirmess', 'ROCR', 'spdep', and 'vegan' (Sing et al. 2005, Goslee and Urban 2007, Bivand and Piras 2015, Oksanen et al. 2015, Dray et al. 2016, Giraudoux 2016, and Hijmans et al. 2016).

Results

Autocorrelation

At a lag distance of <20 m, all but five species were significantly ($\alpha=0.05$) autocorrelated, averaging a Moran's I of 0.57. Most species were autocorrelated at lag distances up to 1 km

(Table 3.1). Despite this, environmental conditions were generally only weakly spatially correlated, as indicated in the Mantel correlogram shown in Figure 3.1. Individual environmental variables were often more strongly spatially correlated than the multivariate measure of environmental conditions, particularly at smaller distance classes (Figures 3.1 and 3.2). Though these statistics show only data from 100 m² spatial grain sizes, similar trends were observed at 1000 m² and full hectare grain sizes (data not shown). Dispersal categories did not differ significantly in spatial autocorrelation, though locally dispersed taxa generally had stronger autocorrelation at 0-20 m lag distance (mean Moran $I=0.61$) than wind or vertebrate dispersed taxa (mean Moran I 0.58 and 0.51, respectively).

MaxEnt models

Though the predictive power (AUC) of spatial MaxEnt models was usually greater than corresponding non-spatial models, the difference was only significant ($\alpha \leq 0.05$) at module scales, a pattern driven by locally dispersing species (Wilcoxon V 2766, $p < 0.01$). Among the most frequently important environmental variables in MaxEnt models were bedrock formation, surficial deposits, disturbance history (including old growth, settlement, and logging), soil mapping unit, and dominant series. When spatial and connectivity variables were also used in the models, Moran eigenvectors and patch, stream, and network connectivity displaced some environmental variables in frequency of model importance, though the same environmental variables were still often important. Moran eigenvectors were less frequently important variables at module and plot scales than they were at hectare scales (data not shown). Pairwise comparison of MaxEnt models between hectare, plot and module scales showed that AUC was significantly higher with smaller spatial scales, both for spatial and non-spatial models (Wilcoxon V between hectare and plot scales 1296 for spatial models and 1240 for non-spatial models; between plot

Table 3.1. Moran's I coefficients of autocorrelation ($p \leq 0.05$) for each species in 100 m² modules at lag distances of <20 m (n=192), 20-150 m (n=372), 150-500 m (n=436), 500 m-1 km (n=604), 1-5 km (3472), and 5-10 km (n=3196).

Species	<20 m	20-150 m	150-500 m	500 m-1 km	1-5 km	5-10 km
<i>Actaea pachypoda</i>						
<i>Actaea podocarpa</i>	0.76	0.34		0.76	0.13	
<i>Adiantum pedatum</i>	0.64	0.53		0.64		
<i>Allium tricoccum</i>	0.81	0.29			0.23	
<i>Amelanchier laevis</i>	0.18		0.15			0.70
<i>Amphicarpaea bracteata</i>	0.65	0.36		0.65		0.40
<i>Anemone acutiloba</i>	0.74	0.45	0.22	0.74	0.21	
<i>Anemone quinquefolia</i>	0.59	0.18				
<i>Asarum canadense</i>	0.89	0.33	0.28	0.89	0.12	
<i>Astilbe biternata</i>	0.77	0.31	0.23	0.77	0.17	
<i>Athyrium asplenoides</i>	0.66	0.48	0.16	0.66	0.13	0.20
<i>Betula alleghaniensis</i>	0.61	0.33	0.12	0.61	0.11	
<i>Botrypus virginianus</i>	0.52	0.31		0.52	0.80	
<i>Brachyelytrum erectum</i>	0.31					
<i>Cardamine diphylla</i>						
<i>Carex aestivalis</i>	0.49					
<i>Carex appalachica</i>	0.74			0.74		
<i>Carex digitalis</i> var. <i>digitalis</i>	0.58		0.26			0.50
<i>Carex laxiflora</i>	0.52	0.24		0.52		
<i>Carex plantaginea</i>	0.74			0.74	0.60	0.90
<i>Carex virescens</i>						
<i>Carya glabra</i>	0.41	0.41	0.16	0.41		
<i>Circaea canadensis</i> ssp. <i>canadensis</i>	0.49	0.20	0.20	0.49		
<i>Clintonia umbellulata</i>	0.65	0.42	0.34	0.65	0.25	0.10
<i>Collinsonia canadensis</i>	0.72	0.64	0.14	0.72	0.12	
<i>Conopholis americana</i>	0.75	0.42		0.75	0.50	
<i>Cornus alternifolia</i>				0.11		
<i>Cryptotaenia canadensis</i>	0.57	0.14			0.60	
<i>Cystopteris protrusa</i>	0.70	0.53	0.16			0.13
<i>Dioscorea villosa</i>	0.56	0.46	0.26	0.56	0.22	
<i>Diphylleia cymosa</i>	0.58	0.16				
<i>Dryopteris marginalis</i>	0.75	0.39		0.75	0.14	
<i>Euonymus americanus</i>	0.71	0.65		0.71		
<i>Euonymus obovatus</i>	0.79	0.49		0.79	0.34	
<i>Eutrochium purpureum</i>	0.70	0.35	0.25	0.70	0.17	0.50
<i>Eutrochium steelei</i>	0.55	0.16	0.16	0.55	0.10	
<i>Festuca subverticillata</i>	0.42	0.50		0.42	0.47	
<i>Galearis spectabilis</i>	0.35	0.28		0.35	0.70	
<i>Galium lanceolatum</i>	0.70	0.52	0.40	0.70	0.14	
<i>Geranium maculatum</i>	0.63	0.14			0.16	
<i>Goodyera pubescens</i>	0.41	0.30		0.41		0.27
<i>Hamamelis virginiana</i>	0.48		0.12	0.48	0.20	
<i>Heuchera villosa</i>	0.75	0.14	0.12	0.75		
<i>Houstonia purpurea</i>	0.38					
<i>Huperzia lucidula</i>	0.52					
<i>Impatiens pallida</i>	0.78	0.28	0.11			
<i>Lilium superbum</i>	0.64		0.21	0.64	0.37	0.40
<i>Luzula acuminata</i>	0.45			0.45		

(continued)

Table 3.1. continued

Species	<20 m	20- 150 m	150- 500 m	500 m- 1 km	1-5 km	5- 10 km
<i>Magnolia acuminata</i>	0.47	0.31				
<i>Magnolia fraseri</i>						0.40
<i>Medeola virginiana</i>	0.51	0.29	0.25	0.51		0.14
<i>Micranthes micranthidifolia</i>	0.71	0.13				
<i>Mitchella repens</i>	0.66	0.24		0.66	0.13	
<i>Mitella diphylla</i>	0.66	0.33			0.11	
<i>Monarda didyma</i>	0.49	0.22		0.49	0.19	0.70
<i>Ostrya virginiana</i>	0.80	0.47		0.80	0.60	
<i>Oxalis violacea</i>	0.82	0.64	0.13	0.82	0.38	
<i>Panax quinquefolius</i>	0.52	0.38	0.16	0.52	0.19	0.60
<i>Parthenocissus quinquefolia</i>	0.50	0.45		0.50	0.18	
<i>Persicaria virginiana</i>	0.42	0.42			0.80	
<i>Phegopteris hexagonoptera</i>	0.42	0.34	0.25	0.42		
<i>Phlox stolonifera</i>	0.92	0.68		0.92	0.10	
<i>Phryma leptostachya</i>	0.62	0.57		0.62		
<i>Pilea pumila</i>	0.66					
<i>Podophyllum peltatum</i>	0.75					0.40
<i>Polypodium appalachianum</i>	0.52	0.14	0.17	0.52		
<i>Pycnanthemum montanum</i>	0.69			0.69		
<i>Pyrularia pubera</i>	0.71	0.13	0.21			0.18
<i>Quercus montana</i>	0.51	0.20	0.12			0.50
<i>Robinia pseudoacacia</i>	0.49					
<i>Rubus canadensis</i>	0.47	0.29			0.23	0.40
<i>Sambucus racemosa</i>	0.37				0.50	0.40
<i>Sanguinaria canadensis</i>	0.79	0.55	0.20	0.79	0.32	
<i>Sanicula odorata</i>	0.82	0.33			0.22	
<i>Sanicula trifoliata</i>	0.38	0.38	0.15	0.38	0.13	
<i>Sassafras albidum</i>	0.73	0.45	0.35	0.73	0.70	
<i>Sceptridium dissectum</i>	0.37					
<i>Sedum ternatum</i>	0.71	0.62	0.32			
<i>Smilax glauca</i>	0.52	0.42				
<i>Smilax herbacea</i>	0.68	0.49	0.18	0.68	0.24	0.24
<i>Solidago flaccidifolia</i>	0.44	0.33		0.44	0.10	
<i>Stachys nuttallii</i>	0.26					
<i>Symphyotrichum cordifolium</i>	0.51	0.26	0.13	0.51	0.20	
<i>Thalictrum clavatum</i>	0.38					
<i>Thalictrum thalictroides</i>	0.95	0.65	0.21			0.50
<i>Thaspium trifoliatum</i>	0.62	0.25		0.62		
<i>Thelypteris noveboracensis</i>	0.75	0.26	0.16	0.75		0.24
<i>Trillium grandiflorum</i>	0.42	0.17			0.50	
<i>Uvularia grandiflora</i>	0.75	0.33	0.17	0.75	0.14	
<i>Uvularia perfoliata</i>	0.42	0.18			0.60	
<i>Veratrum parviflorum</i>	0.79	0.57		0.79		
<i>Viburnum acerifolium</i>	0.45					
<i>Vitis aestivalis</i>	0.70	0.46		0.70		

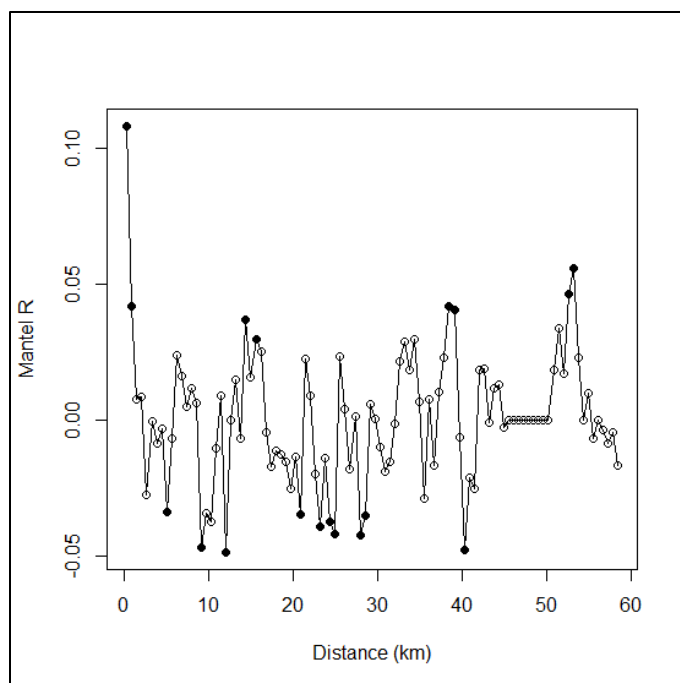


Figure 3.1. Multivariate Mantel correlogram showing autocorrelation of continuous environmental variables at 100 m² sample locations. Filled circles indicate Mantel R values that are significant at $p \leq 0.05$ tested by permutation.

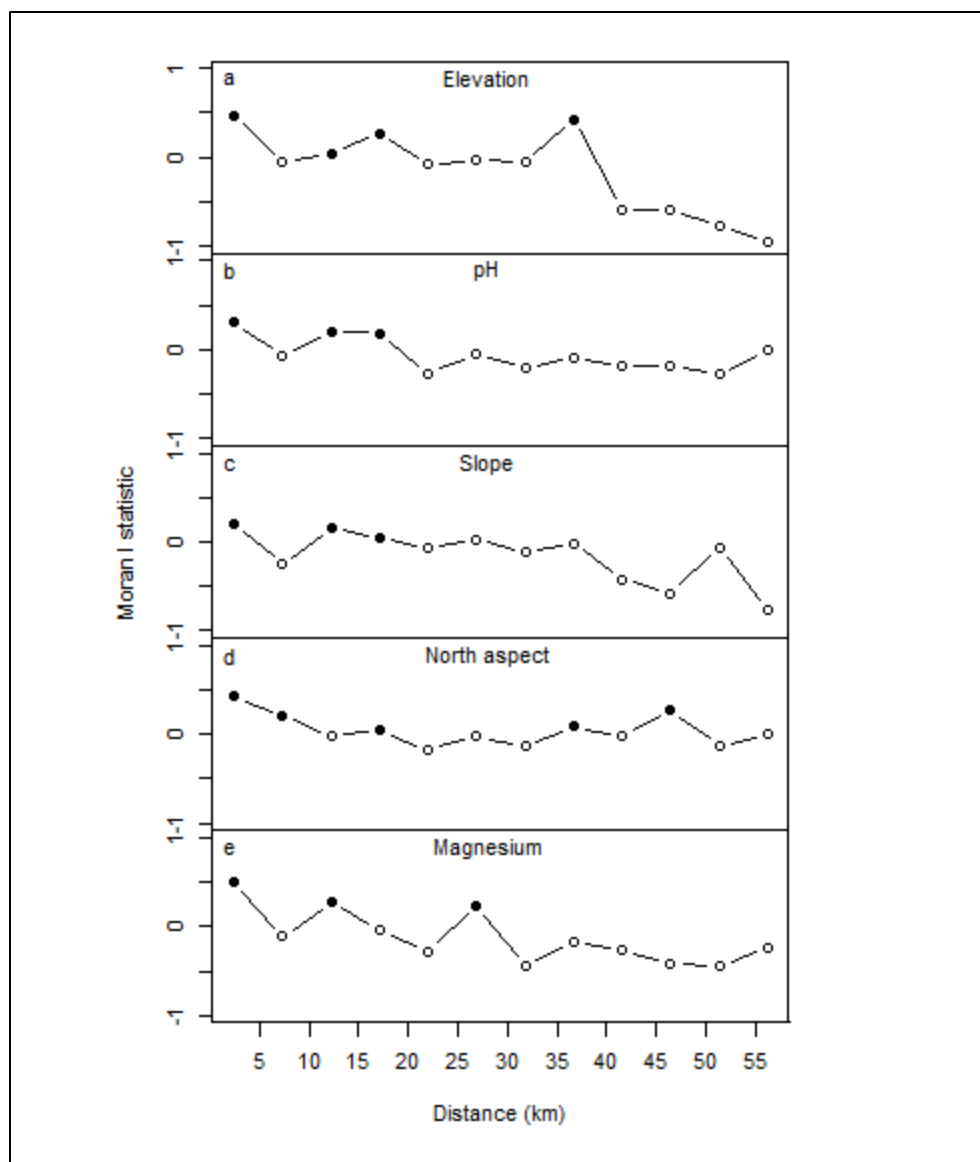


Figure 3.2. Moran's I spatial correlograms for several environmental variables showing spatial autocorrelation at small distance classes using small sampling grains (modules).

and module scales 1563 for spatial models and 1537 for non-spatial models; $p \leq 0.01$).

Differences in model performance between dispersal categories were minimal, though non-spatial MaxEnt models had significantly higher AUC for vertebrate dispersed taxa than wind dispersed taxa at both module and plot scales (Kruskal-Wallis χ^2 7.65 and 6.67 respectively, $p \leq 0.05$).

Logistic regression models

Models including an autocovariate performed significantly better than corresponding models including only environmental variables as predictors at all three spatial scales (Wilcoxon V 2897 for modules, 2054 for plots, and 2306 for hectares, $p \leq 0.05$). Both spatial and non-spatial models increased in AUC with decreasing sampling scale (Wilcoxon V between hectare and plot scales 1512 for spatial models and 1341 for non-spatial models; between plot and module scales 1482 for spatial models and 1729 for non-spatial models; $p \leq 0.05$). Differences between spatial and non-spatial models were significantly greater at module scales than at plot scales (Wilcoxon V 2515, $p < 0.05$), but were not different between dispersal categories, though AUC was higher for vertebrate dispersed taxa than wind dispersed taxa at plot scales for both spatial and non-spatial models (Kruskal-Wallis χ^2 7.82 and 6.25 respectively, $p \leq 0.05$). The addition of an autocovariate significantly reduced the spatial autocorrelation of residuals for many species, particularly at short distances (Table 3.2). The most dramatic reductions (≥ 0.5) at lag distances of less than 20 meters are disproportionately seen among locally dispersed taxa, though the reduction in Moran's I in spatial models did not significantly differ between dispersal categories. Comparison between autocorrelation coefficients in Tables 3.1 and 3.2 indicates that though environmental variables often accounted for species autocorrelation, many species would remain autocorrelated especially at small scales without the addition of an autocovariate.

Table 3.2. Differences in spatial autocorrelation of residuals between spatial and non-spatial logistic regression. Values shown are the reduction in Moran's I coefficients ($\alpha=0.05$) with the addition of an autocovariate term at lag distances as shown in Table 3.1. Major dispersal categories are indicated as v, vertebrate; w, wind; and l, local. Vacant fields indicate that the residuals of non-spatial models were not autocorrelated in the first place.

Species	Dispersal Group	<20 m	20-150 m	150-500 m	500 m-1 km	1-5 km	5-10 km
<i>Actaea pachypoda</i>	v						
<i>Actaea podocarpa</i>	l	0.53				0.07	
<i>Adiantum pedatum</i>	w						
<i>Allium tricoccum</i>	l	0.68				0.06	
<i>Amelanchier laevis</i>	v						
<i>Amphicarpaea bracteata</i>	l	0.08					
<i>Anemone acutiloba</i>	l	0.35	0.15	0.12		0.09	
<i>Anemone quinquefolia</i>	l	0.33				0.04	
<i>Asarum canadense</i>	l						
<i>Astilbe biternata</i>	l	0.43			0.05		
<i>Athyrium asplenoides</i>	w						
<i>Betula alleghaniensis</i>	w						
<i>Botrypus virginianus</i>	w						
<i>Brachyelytrum erectum</i>	v						
<i>Cardamine diphylla</i>	l						
<i>Carex aestivalis</i>	l	0.76					
<i>Carex appalachica</i>	l				0.03		
<i>Carex digitalis</i> var. <i>digitalis</i>	l						
<i>Carex laxiflora</i>	l	0.79					
<i>Carex plantaginea</i>	l	0.30					
<i>Carex virescens</i>	l					0.01	
<i>Carya glabra</i>	v		0.14			- 0.05	
<i>Circaea canadensis</i> ssp. <i>canadensis</i>	v	0.21	0.18	0.11	- 0.01		
<i>Clintonia umbellulata</i>	v						
<i>Collinsonia canadensis</i>	l	0.27		0.12			
<i>Conopholis americana</i>	v	0.87					
<i>Cornus alternifolia</i>	v						
<i>Cryptotaenia canadensis</i>	l						
<i>Cystopteris protrusa</i>	w	0.15					- 0.04
<i>Dioscorea villosa</i>	w	0.54					
<i>Diphylleia cymosa</i>	v						
<i>Dryopteris marginalis</i>	w	0.52	0.21	0.20			
<i>Euonymus americanus</i>	v	0.51	0.13				
<i>Euonymus obovatus</i>	v	0.55	0.35			0.19	
<i>Eutrochium purpureum</i>	w					0.02	
<i>Eutrochium steelei</i>	w						
<i>Festuca subverticillata</i>	l						
<i>Galearis spectabilis</i>	w						
<i>Galium lanceolatum</i>	v	0.28	0.26	0.16	0.13	0.05	
<i>Geranium maculatum</i>	l						
<i>Goodyera pubescens</i>	w	0.15					0.02
<i>Hamamelis virginiana</i>	l						
<i>Heuchera villosa</i>	w						
<i>Houstonia purpurea</i>	w						
<i>Huperzia lucidula</i>	w						

(continued)

Table 3.2. continued

Species	Dispersal Group	<20 m	20-150 m	150-500 m	500 m-1 km	1-5 km	5-10 km
<i>Impatiens pallida</i>	l						
<i>Lilium superbum</i>	w	0.60		0.1	0.17	0.05	
<i>Luzula acuminata</i>	l					- 0.05	0.12
<i>Magnolia acuminata</i>	v						
<i>Magnolia fraseri</i>	v				- 0.05		
<i>Medeola virginiana</i>	v		0.05		0.08		
<i>Micranthes micranthidifolia</i>	l						
<i>Mitchella repens</i>	v	0.25		0.12			
<i>Mitella diphylla</i>	l		- 0.01				
<i>Monarda didyma</i>	l						
<i>Ostrya virginiana</i>	w	0.35			0.05		
<i>Oxalis violacea</i>	l	0.66	0.17		0.09	0.08	
<i>Panax quinquefolius</i>	v	0.18		0.15		- 0.02	0.01
<i>Parthenocissus quinquefolia</i>	v						
<i>Persicaria virginiana</i>	v						
<i>Phegopteris hexagonoptera</i>	w						
<i>Phlox stolonifera</i>	l	0.96					
<i>Phryma leptostachya</i>	v	0.27	0.26				
<i>Pilea pumila</i>	w	0.67					
<i>Podophyllum peltatum</i>	v	0.96				- 0.04	
<i>Polypodium appalachianum</i>	w	0.30	0.13		0.01		
<i>Pycnanthemum montanum</i>	l	0.71					
<i>Pyrularia pubera</i>	v						0.03
<i>Quercus montana</i>	v						
<i>Robinia pseudoacacia</i>	w						
<i>Rubus canadensis</i>	v						
<i>Sambucus racemosa</i>	v				0.01	- 0.05	
<i>Sanguinaria canadensis</i>	l	0.52	- 0.12				
<i>Sanicula odorata</i>	v	0.28	0.17			- 0.06	
<i>Sanicula trifoliata</i>	v					0.05	
<i>Sassafras albidum</i>	v						
<i>Sceptridium dissectum</i>	w	0.31					
<i>Sedum ternatum</i>	w	0.23	0.40	0.13			
<i>Smilax glauca</i>	v		0.12				
<i>Smilax herbacea</i>	v						
<i>Solidago flaccidifolia</i>	w						- 0.02
<i>Stachys nuttallii</i>	l						
<i>Symphyotrichum cordifolium</i>	w						
<i>Thalictrum clavatum</i>	l						
<i>Thalictrum thalictroides</i>	l						
<i>Thaspium trifoliatum</i>	l	0.21					
<i>Thelypteris noveboracensis</i>	w	0.22					
<i>Trillium grandiflorum</i>	v		0.11				
<i>Uvularia grandiflora</i>	l	0.03					
<i>Uvularia perfoliata</i>	l						
<i>Veratrum parviflorum</i>	w	0.36					
<i>Viburnum acerifolium</i>	v						
<i>Vitis aestivalis</i>	v	0.43	0.52				

General trends

Average AUC varied from 0.568 to 0.737, depending on spatial scale, model type, and inclusion of spatial predictors. The addition of spatial predictors increased AUC for most species in both types of model, with 50-64% of species distribution models improving at least somewhat. MaxEnt models generally had higher AUC than either spatial or non-spatial logistic regression models, though the addition of an autocovariate to logistic regression models lead to a higher performance increase relative to the addition of spatial variables to MaxEnt models (Figure 3.3). Average change in AUC with spatial predictors ranged from 0.005 to 0.011 in MaxEnt models and from 0.019 to 0.034 in Logit models, where the smallest average change was at plot scales in both cases, but the pairwise difference between module and plot scales was only marginally significant in Logit models. At module scales, sample size was significantly correlated ($p < 0.05$) with AUC for each type of analysis, where most models that performed no better than random ($AUC \leq 0.5$) were of species that occurred in less than 6% of modules. Though there were no statistically significant differences between dispersal categories in model improvement with the addition of spatial predictors at any scale, locally dispersed species were most frequently improved compared to wind and vertebrate dispersed species, particularly in MaxEnt models and at hectare scales (Figure 3.4).

Discussion

Addition of spatial predictor variables improved species distribution models for most species, but the change was generally minimal. In the case of MaxEnt models, this was likely because many of the spatial patterns among the most important environmental variables (e.g. geology, soil, disturbance history) were also represented by spatial variables, such that the importance of environmental variables in themselves decreased in the presence of spatial

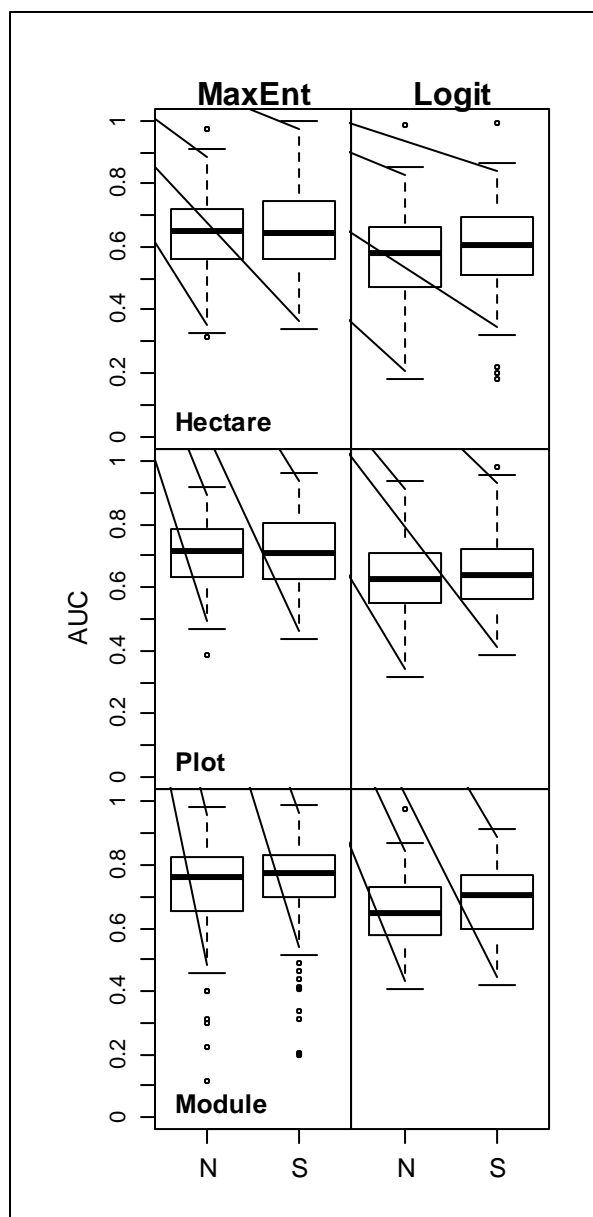


Figure 3.3. Model performance (AUC) for non-spatial (N) and spatial (S) models at hectare, plot (1000 m²), and module (100 m²) scales. MaxEnt models are on the left and logistic regression (logit) models are on the right.

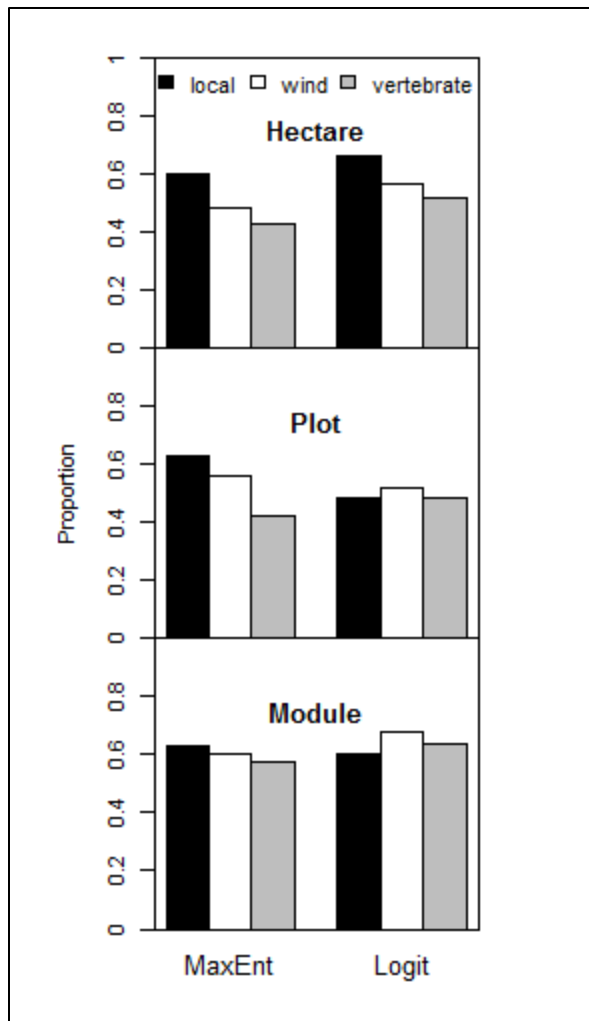


Figure 3.4. Proportions of species in each dispersal category that were improved by the addition of spatial predictors to species distribution models at each spatial scale.

predictors (Phillips et al. 2006). Despite the overall weaker performance among logit models than among MaxEnt models, model improvement with the addition of an autocovariate was more dramatic. This is likely because MaxEnt is overall a more robust modelling technique that can fit complex relationships between predictors and species, and because the calculation of the autocovariate used in logistic regression relies directly on autocorrelation of the species rather than on variables representing spatial pattern that may or may not be correlated with environmental predictors (Elith et al. 2006, Dormann et al. 2007). Because spatial pattern was incorporated into the two types of model in different ways, it remains to be seen exactly which combination of spatial variables and model type would optimize the predictive power of species distribution models among many species, because each species has unique spatial patterns and responses to environmental gradients. One study suggests that logit models perform better than MaxEnt and MEM spatial variables explain more variation in species occurrence than autocovariates, but that study only reflected the distribution of one invasive species (Václavík et al. 2012). In contrast, the present study suggests that for many species, the non-parametric MaxEnt modelling technique has higher predictive power based on environmental gradients despite the fact that it does not incorporate absence data, but that the use of known absences in calculation of an autocovariate can improve model performance. This is particularly true at small scales, where the sampling interval reflects clumped spatial distributions.

One important conclusion from MaxEnt models was that for most species, both spatial and environmental variables extracted from Geographic Information Systems (GIS) are far more important than direct measurement of soil nutrients for predicting occurrences. This outcome is likely system specific, as the availability of quality GIS maps of geology, soil, streams, and vegetation is particularly high for national parks in general and GRSM in particular. In contrast,

because logistic regression requires transformation of mapping units to multiple dummy variables, most of the important predictors were continuous variables derived from soil nutrient analysis. In general, the number of important predictors for logit models decreased with increasing sampling scale, and the categorical GIS variables were only important predictors at plot and module scales. Because GIS variables were of such strong importance in MaxEnt models, and because MaxEnt models were largely more powerful than logit models, the use of high quality GIS variables in landscapes where they are available may be sufficient to accurately model many species distributions without the extra cost and effort of soil sample nutrient analysis.

Sampling scale affects the performance of species distribution models because of how environmental variables are distributed across space, and because the probability of occurrence of any given species increases with spatial scale. Many species that are frequent but not necessarily locally abundant are more likely to be documented at hectare scales, where local environmental conditions are most heterogeneous. In addition, habitat heterogeneity at larger scales can result in mass effects, where species can occasionally persist in suboptimal conditions due to proximity to appropriate habitat (Shmida and Wilson 1985). In the Great Smoky Mountains in particular, steep environmental gradients and topographic heterogeneity mean that species adapted to somewhat drier habitats are often upslope and in fairly close proximity to mesic coves (Whittaker 1956). In combination with the fact that the environmental variables measured at hectare scales were often averaged across space and between smaller scale plots, topographic heterogeneity and mass effects are the likely explanation for lower predictive power at broader sampling scales. The spatial scales of autocorrelation of species (Table 3.1) contribute to the differences between spatial and non-spatial model performance because many species are

clumped at small scales due to dispersal limitation and asexual reproduction, and because sampling at broader scales reflects habitat connectivity and landscape heterogeneity (Plotkin et al. 2002, Seidler and Plotkin 2006, Shen et al. 2009). The sampling scheme of paired adjacent modules and hectares stratified across several levels of habitat connectivity was intended to capture these possible sources of spatial autocorrelation, and so could explain why the differences between spatial and non-spatial models were greatest at module scales, particularly for logit models, where inclusion of an autocovariate based on both distance and connectivity accounted for a significant amount of small scale spatial autocorrelation for many species (Table 3.2).

Though many species share common types of dispersal vectors, differences between species in dispersal capacity in this study appear to be a fairly minor factor in the predictive power of species distribution models, which may also relate to differences in other life history characteristics, how species respond to environmental gradients, and how frequent they are across the landscape (Guisan and Thuiller 2005, Moore and Elmendorf 2006, Dullinger et al. 2011). This study displays some trends in differences in model performance among species groups, particularly that non-spatial models of vertebrate dispersed taxa often have higher predictive power than models for other species, and that spatial predictors are especially useful in modelling species that have restricted dispersal. Despite the fact that these trends among different species groups were not strong, no other way of categorizing species based on life history traits or commonness yielded any observable trends (data not shown). Because dispersal kernels were not measured explicitly (e.g. Dullinger et al. 2011, Boulangéat et al. 2012) but generalized based on morphology, it is possible that multiple dispersal vectors obscure any differences between dispersal methods in distribution (Ozinga et al. 2004). In particular, seed and

spore dispersal may have been facilitated by stream flow, as streams are a central part of mesophytic cove habitats (Whittaker 1956). This effect may be especially prominent among species that do not have any particular modification for dispersal, but are found predominantly in seepages and along streams, such as *Thalictrum clavatum* and *Monarda didyma* (Weakley 2015).

In recent years, there have been calls to consider dispersal processes in the construction of species distribution models, but spatial processes such as dispersal are most often used for mobile animal species rather than for sessile plants (Guisan and Thuiller 2005, Soberón and Peterson 2005, Elith and Leathwick 2009). Models that account for spatial processes have focused on reducing the autocorrelation of model residuals in order to more accurately predict the distribution of individual species rather than as a tool to discern common processes affecting the distribution of many species (Keitt et al. 2002, Lichstein et al. 2002, Dormann et al. 2007). Some studies have shown that accounting for spatial processes such as dispersal and connectivity improves models for many species, but these studies either did not evaluate differences in dispersal ability among species (Bahn and McGill 2007), or used dispersal kernels as a measure of connectivity (Dullinger et al. 2011, Boulangeat et al. 2012). In contrast, this study compares the performances of many models among a large number of species as a means to evaluate the importance of dispersal morphology, habitat connectivity, and sampling scale in spatially correlated species distributions.

Though several methods have been proposed to account for spatial pattern and autocorrelation in species distribution models, spatial predictors are often based on a single specified neighborhood cutoff, while few studies include multiple levels of potential connectivity (Dormann et al. 2007, Foltête et al. 2012). Habitat connectivity is a complicated variable that depends on the dispersal capacity and environmental tolerance of the species in question. It is

therefore difficult to explicitly measure its importance without *a priori* knowledge of each species' ecological limitations and dispersal kernels (Hansson 1991). Despite these difficulties, the present study shows that it is possible to account for connectivity in a way that is applicable to many species by assuming that most common species in a community share similar climatic, topographic, and edaphic requirements. Among the obvious drawbacks of this approach are the fact that each species has both a unique response to environmental conditions and a unique dispersal kernel, and the perennial problem that it is impossible to eliminate the possibility that any spatial or connectivity variables that emerge as important simply reflect an unmeasured but spatially correlated environmental variable (Greene and Calogeropoulos 2002, Fortin and Dale 2005). In using several levels of connectivity as predictors in MaxEnt models and in using those levels as weights in calculation of an autocovariate, the methods used here depart somewhat from simply using the spatial pattern displayed by individual species (Augustin et al. 1996, Dray et al. 2006, Dormann et al. 2007). However, by applying a general connectivity model to multiple species, we can identify the species that may be vulnerable to regional extinction in the face of landscape changes, and the scales at which connectivity is important. This allows us to make more comprehensive assessments for conservation of community-level biodiversity rather than focusing on only one species of concern.

The results shown here reflect the complicated relationship between dispersal and environmental heterogeneity, suggesting that although environmental variables are important in determining species distributions, spatial variables are often more important because they represent both spatially structured environmental conditions and autocorrelation caused by endogenous processes such as dispersal limitation (Legendre 1993, Fortin and Dale 2005). This study also suggests that the incorporation of spatial predictors is more important at small scales

and for taxa without adaptations to long distance dispersal. Explicitly measuring the effects of dispersal is difficult without detailed knowledge of each species' dispersal kernel, particularly because it is compounded by the many ways species differ in life history traits and how they respond to environmental gradients (Grubb 1977, Nathan et al. 2012). Though this study was inconclusive on exact generalizations on distribution that can be made only on the basis of dispersal morphology, it is clear that many species show spatial relationships that cannot purely be accounted for by a multitude of environmental variables, and that morphology is an important determinant in species' dispersal and distribution across multiple scales (Nekola and White 1999, Tamme et al. 2013). In light of the importance of spatial predictors in species distribution models, this study highlights the importance of maintaining habitat connectivity in the face of global climate change. Species of mixed mesophytic habitats of the southern Appalachian Mountains may be especially susceptible to local or regional extinction because of high endemism, cool climate, and a legacy of habitat destruction (Estill and Cruzan 2001, Elliot et al. 2014). Future research should include more accurate models of dispersal kernels in addition to climate change projections in species distribution models (Travis and Dytham 2012) to identify the species most under threat, and to make informed conservation decisions to protect plant populations and communities from the compound effects of climate change, habitat destruction, and fragmentation.

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CHAPTER 4. INTERPRETATION OF NON-RANDOM PATTERNS IN PLANT COMMUNITIES: EFFECTS OF SPATIAL AND ECOLOGICAL PROCESSES

Introduction

Understanding patterns in nature is one of the predominant goals in the science of ecology, but the many interacting processes that affect species' interactions make it difficult to discern any potential influence from a multitude of others (Götzenberger et al. 2012). Looking for patterns in species occurrences and co-occurrences among local communities has long been a focus for testing ecological assembly theory. Since Diamond (1975) proposed the existence of assembly "rules" that constrain species occurrence and co-occurrence, many studies have attempted to demonstrate that non-random patterns in communities result from competitive exclusion. One problem with this logic is that, as Weiher and Keddy (1999) so eloquently state, "asking if there is pattern in nature is akin to asking if bears shit in the woods", explaining that the mere documentation of a pattern is not the same as identifying causal mechanisms. Despite this and other warnings about interpretation of non-random patterns of community composition, multiple studies use comparisons to null community models of random occurrences to infer that either habitat variability or interspecific interactions are driving observed patterns of segregation or aggregation of species (Weiher and Keddy 1995, Gotelli and McCabe 2002, Götzenberger et al. 2012).

Community assembly theory emphasizes species sorting and habitat filtering, both of which assume that dispersal limitation is a regional rather than local process, and that once

species are members of a regional species pool, communities are assembled based on deterministic niche relationships and adaptation to the local environment (Zobel et al. 1998, Leibold et al. 2004, Weiher et al. 2011). Many studies either ignore dispersal or assume that it is a stochastic effect at local scales and is more important in explaining regional diversity patterns (Jenkins 2006, Ricklefs 2008, Chase and Myers 2011). The dichotomies between both local versus regional and deterministic versus stochastic processes are both relative and simplistic, because dispersal limitation occurs on local scales as well, and is a spatially explicit process (Bullock et al. 2002, Levine and Murrell 2003, Ricklefs 2008). Definitions of "stochastic" processes vary, but usually refer to random or unpredictable processes, sometimes within a probability distribution (Hubbell 2001, Chase and Myers 2011, Gravel et al. 2011, Weiher et al. 2011). Opinions vary as to whether dispersal is a purely stochastic process; however, dispersal in the real world is certainly not random in space and also differs between species. Even neutral models that assume that species' dispersal capacities are equivalent can produce non-random patterns of community composition (Ulrich 2004, Bell 2005). As such, non-random patterns of community composition cannot rule out the effects of dispersal limitation.

Some modifications of the null model paradigm, in which species occurrences are randomized across all sample locations, can be useful in indicating species sorting, habitat filtering, or limited dispersal. These methods include comparing community trait dispersion rather than species composition to null models (Weiher et al. 1998), holding environmental conditions constant (Elwood et al. 2009), or constructing null models by randomizing species occurrences in nested and spatially restricted subsets (Cornell et al. 2007). Other studies have suggested comparing observed patterns to those produced from a neutral (rather than null) model, but few have looked specifically at how differences in dispersal affect community co-

occurrence patterns (Gotelli and Ulrich 2012, Götzenberger et al. 2012, Trejo-Varocio and Arita 2013). Without a practical way to estimate accurate dispersal parameters for all plant species in a natural community, I here group species by dispersal morphology and evaluate differences in departures from randomness in co-occurrence of species and turnover among samples. In addition, I compare results from three different sampling scales in an effort to understand how intraspecific aggregation changes with spatial scale. If dispersal is truly more important at broad spatial scales, dispersal limited species should be more likely to show nonrandom patterns at large sampling scales, all else being equal. To discern the effects of spatial processes such as dispersal and connectivity from environmental control on co-occurrence patterns, I use variation partitioning coupled with the β_{RC} metric proposed by Chase et al. (2011) to measure pairwise departures from randomness.

Methods

Vegetation

Vegetation in mixed mesophytic communities of the Great Smoky Mountains National Park (GRSM) was sampled in 47 hectares stratified by five levels of habitat connectivity based on the vegetation map of Madden et al. (2004). Each hectare measured 100 by 100 m and contained two 20 by 50 m plots, generally in diagonal corners. Each plot, in turn, contained four intensively sampled 10 by 10 m modules (an approach modified from Peet et al. 1998 including a species list and cover classes but without nested corners), and soil samples were collected from two of these. All vascular plant species were recorded at the three spatial scales of hectares (10000 m²), plots (1000 m²), and intensively sampled modules (100 m²). All species were grouped into categories based on dispersal morphology, based on the assumption that plants with similar dispersal syndromes have similar dispersal distances (van der Pijl 1972, Vittoz and

Engler 2007, Tamme et al. 2014). Vertebrate dispersal categories included seeds or fruits dispersed by endozoochory (eaten by vertebrates), epizoochory (attached to the fur or feathers of vertebrates), or dyszoochory (hoarding by small mammals or blue jays in caches). Anemochory, or dispersal by wind, included seeds or fruit that had plumed appendages for floating through the air, winged appendages for gliding, seeds that are so tiny and light that they could be blown away by wind, and ferns and lycophytes that disperse by spores. More locally dispersed categories included seeds dispersed by ants and seeds or fruit without any morphological adaptations for dispersal. Using the three broad dispersal categories (vertebrate, wind, and local dispersal), and nine narrow categories, I analyzed patterns in occurrence at three spatial scales (hectare, plot, and module), and compared the groups in terms of differences from randomly assembled plant communities. Because non-random patterns may also be affected by size and growth habits at different scales, I also investigated patterns within different growth forms including graminoids, herbs, shrubs, small trees, trees, and vines.

Environmental variables

Soil samples were collected in the top 10 centimeters of two intensively sampled modules in each plot and analyzed for extractable micro- and macronutrients using a Mehlich III extraction technique (Mehlich 1984) by Brookside Labs, New Bremen, Ohio. In addition, several variables were extracted for each sample unit using ArcGIS 10.3, including soil mapping unit, dominant series, subgroup, and order (USDA 2009); bedrock formation, group, and surficial deposits (Southworth et al. 2012); disturbance history (Pyle 1985); elevation, slope, and aspect (NPS 2011); topographic indices of soil moisture (NPS 2013, 2014); and temperature parameters (Fridley 2011). All variables were extracted within a 10-m buffer zone along the edges of each sample unit. Aspect was first transformed to continuous unidirectional variables (Beers et al.

1966, Clark et al. 1999), then each of the continuous variables was averaged for each sample unit. To account for topographic heterogeneity, variance in Beers aspect was also calculated (Beers et al. 1966). For variation partitioning, categorical variables (soil type, geology, and disturbance) were transformed to dummy variables.

Measuring non-random patterns

I used two metrics to indicate non-random patterns in the distribution of each species group. Both were based on differences from null community models, which were constructed by randomizing occurrences of each species across the dataset while holding the species richness of each locality and the total occurrences of each species constant (Gotelli 2000, Gotelli and Entsminger 2003, Chase et al. 2011). The *C*-score of Stone and Roberts (1990) measures "checkerboard" distributions where more species pairs avoid each other than expected by chance. Where the original conception of the ecological "checkerboard" was proposed to indicate competitive exclusion (Diamond 1975), Connor and Simberloff (1979) and Stone and Roberts (1990) demonstrate that some "checkerboards" emerge from island-biogeographic processes such as colonization. If individual species show clumped distributions at any scale resulting in part from dispersal, then it would also contribute to a checkerboard pattern. Because *C*-score varies based on the total number of species, I measured the standardized effect size (SES) of *C*-score in order to compare groups of species that are different sizes. Positive SES indicates a greater proportion of species pairs that co-occur less frequently than random (segregation), and negative SES indicates a greater proportion of species pairs that co-occur more frequently than random (aggregated pairwise distributions; Gotelli and McCabe 2002). The β_{RC} metric proposed by Chase et al. (2011), in contrast, isn't calculated based on species pairs but on site pairs, and measures the standardized difference from the expected number of shared species given the

diversity of the two plots and the frequency of each species in the dataset. For each species group at each scale, I calculated the mean β_{RC} , which increases when communities are more dissimilar to each other than expected, indicating either deterministic processes such as environmental filtering or dispersal limitation (Chase et al. 2011). To calculate both β_{RC} and SES of C-score, I used a swap algorithm to generate 999 simulated datasets, each of which holds species richness than frequency of occurrence constant (Gotelli and Entsminger 2003).

Variation partitioning

Because there is a value of β_{RC} for each pair of sampling locations, it is possible to use variation partitioning to test whether departures from randomness are explained by spatial or environmental variables. To discern these two possibilities, I used both partial Mantel tests and variation partitioning based on distance-based redundancy analysis (dbRDA; Mantel 1967, Smouse et al. 1986, Legendre and Anderson 1999). Both methods quantify the unique contribution of either spatial or environmental explanatory variables while controlling for the other. For each group and scale, I used forward selection to subset the set of possible environmental variables (Dray et al. 2016), and then used these to calculate a distance matrix that indicated pairwise environmental difference between sample locations (Legendre and Legendre 1998) for Mantel tests. In addition, Mantel tests also test the relative importance of spatial processes (including dispersal) by correlating the matrix of β_{RC} with a matrix of the log of spatial distance. To construct spatial predictor variables for variation partitioning by dbRDA, I used principal coordinates of neighbor matrices (PCNM) to model spatial relationships at many scales (Borcard et al. 1992, Borcard and Legendre 2002, Legendre and Anderson 1999, Dray et al. 2006). I also created variables representing habitat connectivity at the scales of habitat patch, network of patches connected by marginally mesophytic habitat, stream drainage, and small and

large river watersheds based on vegetation and stream maps of GRSM (Madden et al. 2004, NPS 2015). These pairwise connectivity metrics ranged from 0 for two locations in the same habitat patch to 5 for two locations in different large river watersheds. Forward selection was used to construct one set of spatial predictors composed of PCNM and connectivity variables, and one set of environmental predictors. Connectivity was not used as a predictor matrix for Mantel tests because it was strongly correlated to spatial distance (Mantel $R > 0.85$) but generally did not have as strong predictive power. All statistical analyses were performed using R (R Core Team 2016) and the packages *ecodist* (Goslee and Urban 2007) and *vegan* (Oksanen et al. 2015).

Results

C-Score

SES increased with spatial grain size and with number of species per group (Table 4.1). Because of the correlation between SES and number of species, in order to discern the effects of group size and group identity, I took 100 random subsets of the total species pool at intervals of 10 species and calculated the C-score SES for those subsets, then compared them to dispersal categories. At hectare and plot scales, species with no dispersal adaptations had relatively lower SES than a majority of random species subsets of similar sizes, though still showed strong patterns of segregation (Figure 4.1, Table 4.1). At module scales, vertebrate dispersed species, particularly endozoochorous species, were more segregated than a majority of random species subsets of similar sizes. Species dispersed by hoarding by small mammals were more spatially segregated than most random subsets at all spatial scales. Graminoids were more aggregated than a majority of random species samples of similar size at hectare and plot scales, and did not have a significant SES at the scale of modules (Table 4.1).

Table 4.1. Standard effect size (SES) of C-Scores at three spatial grain sizes. n.s. indicates not significantly different from random community composition at $\alpha=0.05$; * indicates $p \leq 0.05$; for all other values $p \leq 0.001$.

<i>Species Group</i>	<i># species</i>	<i>Hectare</i>	<i>Plot</i>	<i>Module</i>
All species	396	28.9	16.1	21.4
Broad dispersal categories				
<i>local</i>	170	39.3	23.8	38.2
<i>wind</i>	111	21.5	17.3	16.3
<i>vertebrate</i>	115	23.5	29.2	36.0
Narrow dispersal categories				
<i>none</i>	149	21.4	19.0	25.6
<i>ant</i>	21	4.4	2.8	5.7
<i>plume</i>	29	4.5	3.5	4.9
<i>wing</i>	36	7.3	8.0	4.3
<i>tiny</i>	24	3.4	3.5	3.0*
<i>spore</i>	22	7.0	6.4	2.4*
<i>hoard</i>	15	5.6	8.8	8.5
<i>epizoochory</i>	30	8.1	8.0	4.7
<i>endozoochory</i>	70	16.5	15.7	21.9
Growth forms				
<i>graminoids</i>	57	6.3	3.5	n.s.
<i>herbs</i>	200	36.0	29.2	32.0
<i>shrubs</i>	32	4.1	5.0	4.8
<i>small trees</i>	21	5.8	5.4	n.s.
<i>trees</i>	37	7.2	12.3	11.2
<i>vines</i>	12	3.7	10.0	10.1*

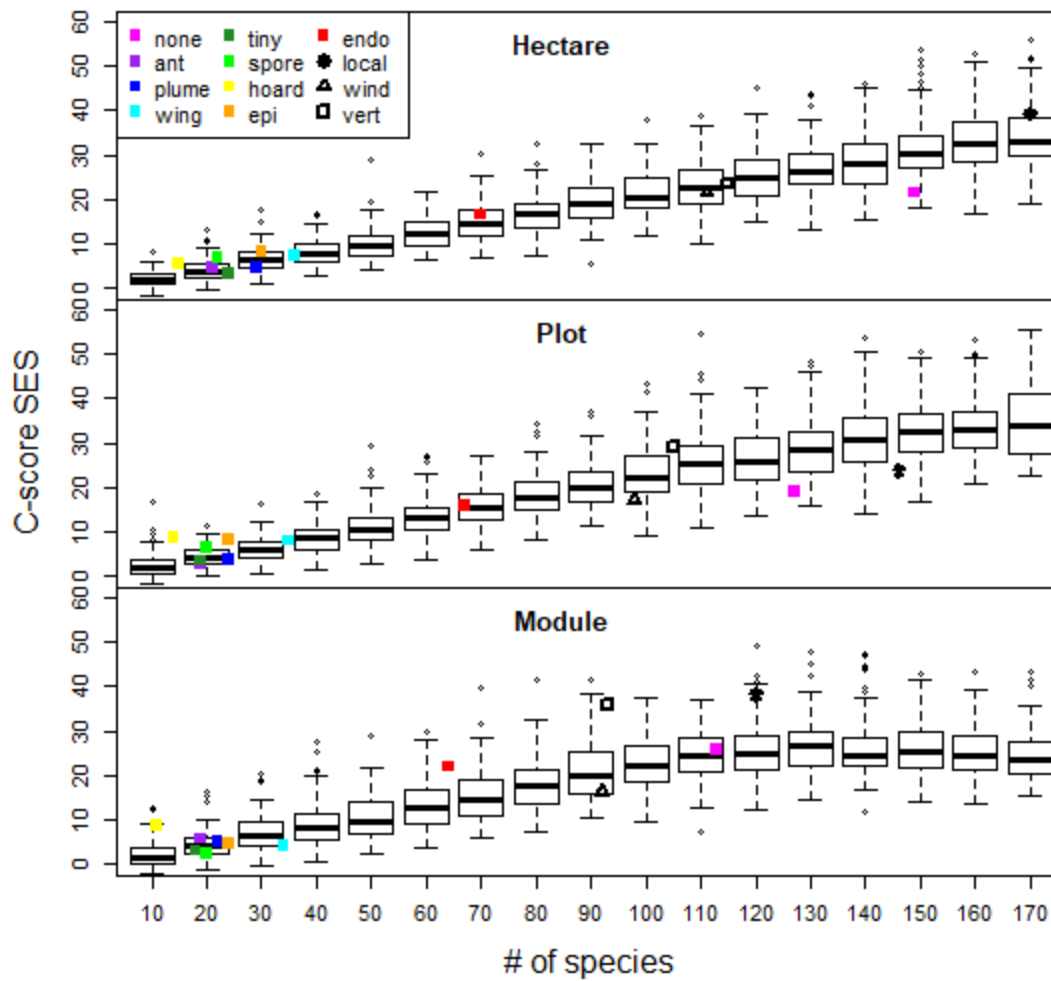


Figure 4.1. C-score SES of random subsets of the dataset in intervals of 10 species (boxplots) superimposed by dispersal categories at three sampling scales. Dispersal categories are indicated as "none" (no dispersal adaptations), "ant", "plume", "wing", "tiny" (seeds ≤ 0.5 mm), "spore", "hoard" (dispersed by small mammals hoarding fruit/seeds in caches), "epi" (epizoochory), "endo" (endozoochory), "local" (including "none" and "ant"), "wind" (including "plume", "wing", "tiny", and "spore"), and "vert" (vertebrate-dispersed species by hoarding, epizoochory, or endozoochory).

β_{RC}

Mean β_{RC} decreased with spatial grain size for all species groups, but also generally decreases with the number of species in each group. The three broad dispersal categories (local, wind, and vertebrate) had similar mean β_{RC} (Table 4.2). Environmental predictors were generally more important than spatial predictors in determining β_{RC} using Mantel tests (Figure 4.2), but spatial predictors were more important with variation partitioning using dbRDA, connectivity, and PCNM variables (Figure 4.3). Though overall variation explained by either spatial or environmental variables increased with spatial scale, space was proportionally more important relative to environmental variables for both methods at small spatial scales. Among dispersal categories, spatial predictors explained more total variation for locally dispersed species than wind or vertebrate dispersed species at most scales using both methods (Figures 4.2 and 4.3).

Discussion

Most species groups at most scales showed non-random patterns, where species pairs tended to be segregated and sampling locations were on average more different than expected by chance. Both metrics indicating non-random patterns were contingent on spatial scale and number of species, though *C*-score SES tended to increase with scale and species number, while mean β_{RC} decreased. It is therefore difficult to compare groups differing in dispersal mechanism in that the size of these groups varied. The category of species with no morphological adaptations to dispersal, for instance, consistently had highest SES among all finer dispersal categories, but also had the most species by far (Table 4.1). While it would be tempting to infer that dispersal-limited species are more likely to show non-random distributions, the SES of endozoochorous species, with morphological adaptations to long-distance dispersal, was the second highest, and was the second-largest group. Comparisons among broad dispersal

Table 4.2. Mean β RC at three spatial grains.

<i>Species Group</i>	<i># species</i>	<i>Hectare</i>	<i>Plot</i>	<i>Module</i>
All species	396	0.54	0.59	0.63
Broad dispersal categories				
<i>local</i>	170	0.57	0.60	0.67
<i>wind</i>	111	0.57	0.61	0.65
<i>vertebrate</i>	115	0.57	0.59	0.66
Narrow dispersal categories				
<i>none</i>	149	0.57	0.61	0.67
<i>ant</i>	21	0.64	0.68	0.75
<i>plume</i>	29	0.70	0.73	0.78
<i>wing</i>	36	0.62	0.63	0.69
<i>tiny</i>	24	0.69	0.79	0.89
<i>spore</i>	22	0.65	0.69	0.73
<i>hoard</i>	15	0.74	0.74	0.76
<i>epizoochory</i>	30	0.70	0.74	0.83
<i>endozoochory</i>	70	0.58	0.62	0.69
Growth forms				
<i>graminoids</i>	57	0.69	0.81	0.93
<i>herbs</i>	200	0.56	0.58	0.65
<i>shrubs</i>	32	0.65	0.71	0.83
<i>small trees</i>	21	0.71	0.81	0.88
<i>trees</i>	37	0.62	0.62	0.67
<i>vines</i>	12	0.78	0.77	0.87

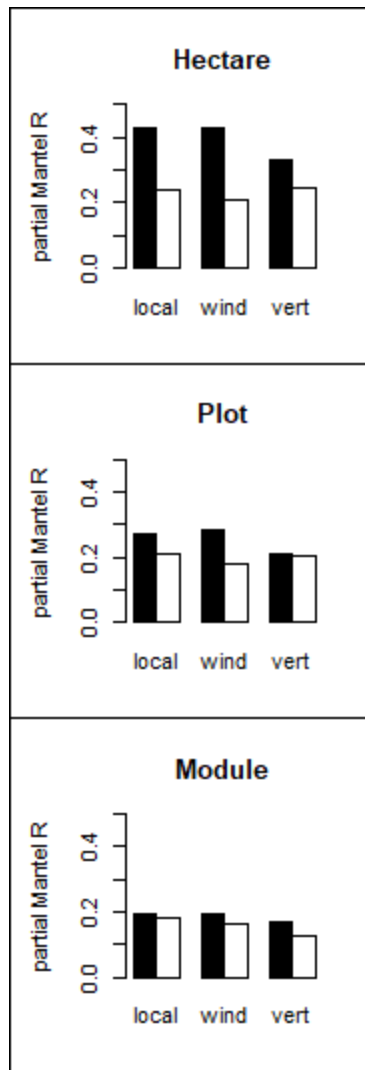


Figure 4.2. Partial Mantel correlation coefficients (R), at three spatial scales compared among broad dispersal categories as defined in Figure 4.1. Black bars show variation explained by environment after controlling for spatial distance; white bars show variation explained by spatial distance after controlling for environmental dissimilarity.

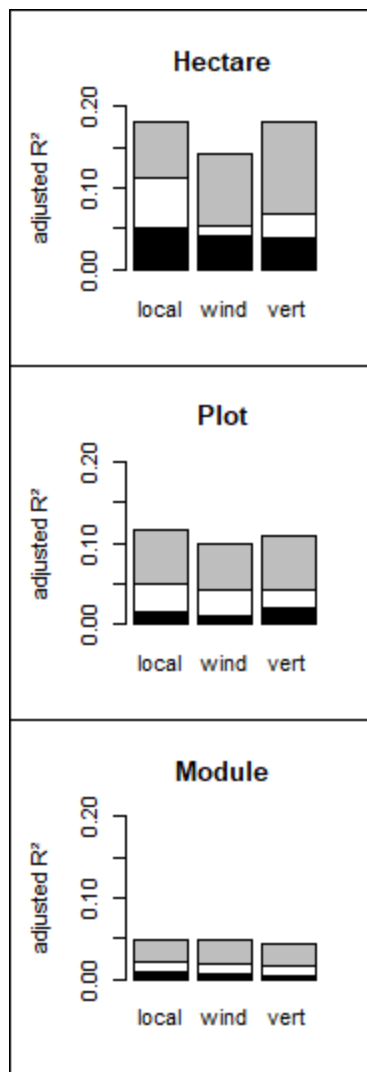


Figure 4.3. Adjusted R² for the contributions of environmental variables (black), spatial variables (white), and spatially correlated environment (grey) for three spatial scales compared among broad dispersal categories (defined in Figure 4.1).

categories are perhaps more useful for comparison, as the size of these groups are more even than the sizes of the smaller and more specific dispersal categories. Interestingly, locally dispersed species had higher SES than all species together at all spatial scales, despite the fact that they are a subset of less than half of the total species pool. Vertebrate-dispersed species had even higher SES at plot and module scales, indicating that other factors may be at play, including the scales of autocorrelation of species of different groups and how they may respond to environmental gradients.

The correlation between species group size, scale, and *C*-Score has been noted by others, including Gotelli and Ulrich (2012), who note that larger datasets almost always reject the null hypothesis of random patterns, and Fayle and Manica (2010) who found that Type I error increases with the number of species and evenness of abundance distributions. In my dataset, rank-frequency distributions showed that locally-dispersed species, particularly species with no dispersal adaptations, had proportionally more rare species than other species groups and more uneven distribution (Figure 4.4). This could explain why species with no dispersal adaptations at hectare and plot scales were not as segregated as most random species subsets of similar sizes, as they are less prone to type 1 error. Alternatively, local dispersal within habitat patches in conjunction with filtering across environmental gradients could lead to this pattern, considering that local dispersal is considered an advantage in patchy but stable habitats across a heterogeneous landscape (Shmida and Ellner 1984, Snyder and Chesson 2002).

The difference between trends of *C*-score SES and β_{RC} with regards to sampling grain and species diversity are difficult to evaluate, though both metrics are calculated based on random community composition among all sample locations. Chase et al. 2011 suggested that sampling among relatively similar habitats should decrease β_{RC} , but that larger sample scales

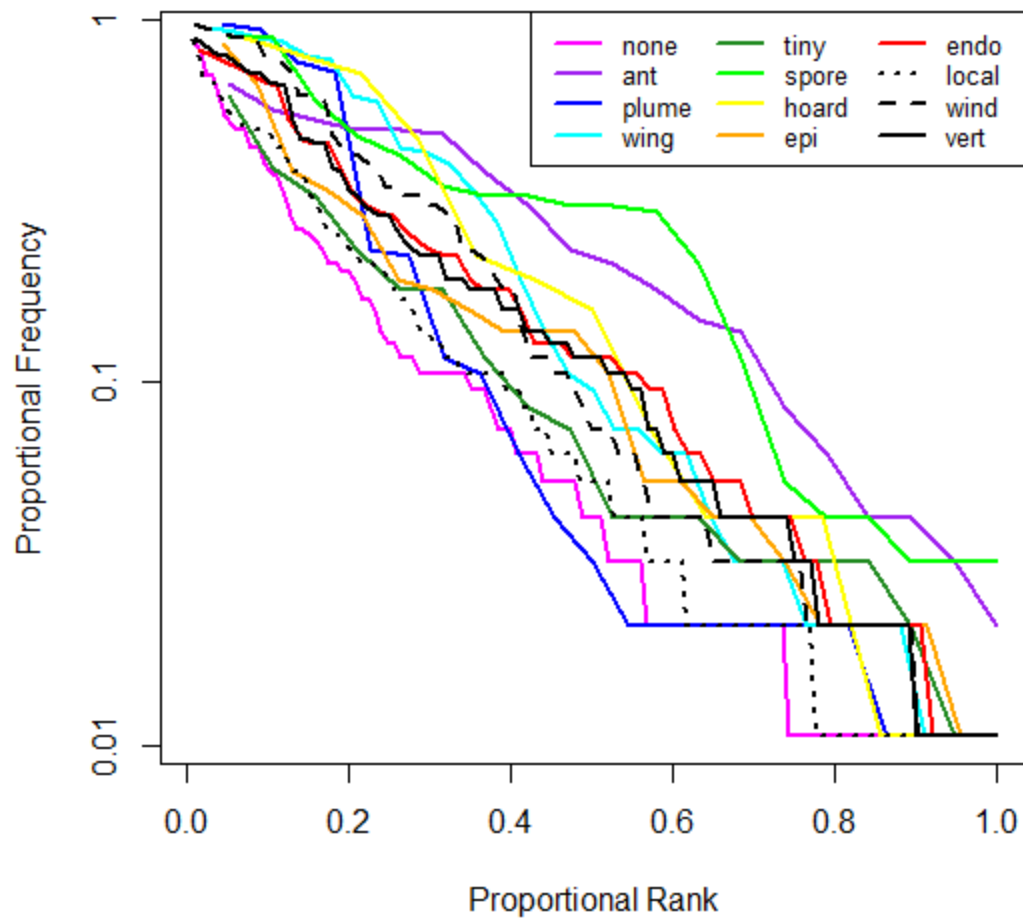


Figure 4.4. Rank-frequency distributions of dispersal categories in hectares, standardized by the richness of each group. Distributions were similar at smaller grain sizes. Dispersal categories are abbreviated as in Figure 4.1.

would increase it as local communities would be compared among a more diverse regional flora. This study found that despite restricting analyses to mixed mesophytic habitats, local community composition was more dissimilar than random for all groups and all scales. Besides dispersal limitation, it is possible that the steep environmental gradients characteristic of montane areas affected this, where even communities that were fairly similar showed trends in species composition related to elevation or nutrient composition (Whittaker 1956). Inclusion of greater habitat heterogeneity and mass effects at larger sampling grains means that a greater percentage of the regional species pool is represented, therefore lowering mean β_{RC} (Shmida and Wilson 1985, Zobel 1997). Conversely, rare species that are not as likely to be sampled at small scales and are spatially isolated from each other may carry heavier influence on the *C*-score metric based on species pairs (Stone and Roberts 1990).

Despite uncertainties in how β_{RC} responds to scale and group diversity, it is certainly a valuable tool for discerning the relative influence of spatial and environmental processes, because it yields a metric for each pair of sample locations, regardless of how far apart or how environmentally distinct they are (Chase et al. 2011). My analyses showed that β_{RC} among locally dispersed species is more strongly related to spatial variables as compared to species with adaptations to wind or vertebrate dispersal (Figures 4.2 and 4.3). Lower total explained variation in β_{RC} at smaller spatial scales likely means that species composition is less predictable and potentially skewed by the number of individuals that can occur within a limited area (Williams 1943). Nonetheless, spatial variables explain a greater proportion of total explained variation at smaller scales, likely because of small-scale spatial clumping due to dispersal limitation or vegetative reproduction.

The results shown here confirm that it is difficult to come to any conclusions regarding community assembly by simply documenting non-random patterns, which may be caused by a multitude of interacting processes (Weiher and Keddy 1999, Götzenberger et al. 2012). The correlation of β_{RC} with spatial and environmental variables is perhaps the most promising approach, showing that spatial processes, after controlling for many possibly confounding environmental influences, had a significant influence on departures from random composition, most particularly for dispersal limited species. Other studies have proposed modifications of the null model approach that either randomized species occurrences in spatially restricted subsets (Cornell et al. 2007) or decoupled frequency and richness patterns compared to null and neutral models (Trejo-Barocio and Arita 2013) in order to discern the effects of habitat variability and dispersal limitation. Comparison among species groups has been minimal, especially within the same sample locations (but see Livingston and Philpott 2010). However, general trends compared among major groups has suggested that more dispersal limited groups are more likely to show non-random patterns (Götzenberger et al. 2012, Trejo-Barocio and Arita 2013).

Importantly, the analyses shown here illustrate the complexities of attempting to separate deterministic and stochastic processes, because spatial processes including dispersal limitation are more probabilistic than random, and contribute to non-random patterns in plant communities. In addition, spatial determinants of non-random patterns were apparent at all spatial scales, suggesting that spatial processes including intraspecific clumping, dispersal, and habitat connectivity affect both small and large scales, rather than the frequent assumption that dispersal limitation is important predominantly at broad scales (Shmida and Wilson 1985, Ricklefs 1987, Chase and Myers 2011). Progress in understanding communities is contingent on recognizing the

complexities of how dispersal processes interact with environmental and competitive processes across spatial scales (Weiher et al. 2011, Leibold et al. 2017).

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CHAPTER 5. INTERACTION BETWEEN DISPERSAL TRAITS AND BIOGEOGRAPHIC PATTERNS IN VASCULAR PLANTS OF MESOPHYTIC HABITATS OF THE SOUTHERN APPALACHIAN MOUNTAINS

Introduction

The composition and diversity of regional floras emerges from the spatial distributions of the ranges of component species. Many factors determine a species' geographic range. Most explanations hinge on environmental factors such as climate or ecological factors including interaction with other species (MacArthur 1972, Brown et al. 1996). It is most commonly assumed that a species' range extent is in equilibrium with its environmental tolerances (e.g. Brown 1984), but population-level processes such as dispersal can affect the dynamics of landscape-scale distributions such as local occurrence (Hanski 1982), and also may play a role in the ability of a species to colonize all appropriate habitat at regional scales (Svenning and Skov 2004, Matlack 2005, Svenning et al. 2008). This may be particularly important in areas affected by climate change associated with recent glaciation. Though the southern Appalachian Mountains were not glaciated, climate cooled across North America during last Pleistocene glaciation, and the mountains served as a major migrational pathway for plant species. This is largely because of their north-south orientation and the spatial proximity of multiple climatic conditions due to topographic heterogeneity. The southern Appalachians are now known as a center of plant diversity and endemism because of both their heterogeneity and their biogeographic history (Harshberger 1911, Braun 1950, Whittaker 1956, Estill and Cruzan 2001).

The biogeographic patterns of southern Appalachian plants derive from events much farther back in time than the Pleistocene, as indicated by the abundance of genera disjunct between eastern North America and eastern Asia, particularly in mesophytic coves, which are the among the most species-rich habitats in the region (Cain 1943, Braun 1950). This intercontinental pattern of generic and ecological similarity likely dates back to the early Tertiary, though the timing of genetic isolation or other processes, such as migration and colonization, varies between taxa (Wen 1999, Tiffney and Manchester 2001, Donoghue and Smith 2004). Thus, current geographic ranges of species are the result of both contemporary and historic dynamics of how each taxon relates to its environment and traverses across space (Brown et al. 1996, Kunin and Gaston 1996, Ricklefs 2008, Wiens 2011). Discerning the relevant dispersal processes from the many contributing factors that have affected geographic range is therefore difficult, but a macroecological approach can characterize trends in how traits, including dispersal morphology, relate to the biogeographic distributions of taxa (Brown 1995, Gaston and Blackburn 2000). Macroecology originally focused on trends in distribution of animal taxa, but many of its methods and theories apply also to plants, despite fundamental differences in growth form, life cycle, movement, and the way they interact with other organisms and the environment (Brown and Maurer 1989, Brown 1995, Blackburn and Gaston 2003). In particular, broad-scale trends in geographic range, frequency, and local abundance can indicate traits related either to ecological specialization or to dispersal, though the former is more often emphasized (Brown 1984, Hanski et al. 1993, Gaston 1996). Here, I specifically evaluate the role of dispersal in affecting broad-scale trends, using a macroecological approach to test whether dispersal-limited plant taxa have more restricted ranges than those with adaptations to long-distance dispersal. To do this, I investigated relationships between dispersal traits, geographic

range, and biogeographic history of plant species in mixed mesophytic forests of the southern Appalachian Mountains.

The ranges of plant taxa can be characterized either by extent or occupancy (Gaston 1996), and on a broader scale, regional occurrence is governed by the biogeographic history of genera and lineages. There are a number of reasons to expect dispersal processes to be related to range extent and occupancy as well as biogeographic history for plants: 1) Metapopulation dynamics predicts that limited dispersal decreases occupancy of habitat patches, contributing to a bimodal frequency distribution of occupancy with many common and many rare species and a positive relationship between local abundance and frequency (Hanski 1982, Hanski et al. 1993); 2) rare, long distance dispersal events account for rapid migration and range expansion from glacial refugia (Cain et al. 1998, Clark et al. 1998); 3) potential and realized ranges differ for many plant species, presumably owing to postglacial migrational lag (e.g. Svenning and Skov 2004, 2007); 4) limited dispersal and isolation can contribute to speciation and therefore patterns of endemism (Cain 1944, Gillespie et al. 2012); 5) occurrence of species in any region is contingent on the historical dispersal processes of ancestral lineages (Manchester 1999, Xiang and Soltis 2001, Donoghue and Smith 2004, Lomolino et al. 2006); 6) dispersal mechanisms can be evolutionary adaptations to the conditions, distribution, and dynamics of appropriate habitat (Levin et al. 2003); and 7) capacity for long-distance dispersal affects the ability of a lineage to migrate between regions, contributing to patterns of distribution and floristic affinity for higher-level taxa (Tiffney 1984, Xiang and Soltis 2001).

The causal mechanisms responsible for range sizes are often linked to a generally positive correlation between distribution and abundance, which is interpreted as resulting either from ecological specialization and the spatial distribution of appropriate habitats, or from

metapopulation dynamics driven by dispersal (Hanski 1982, Brown 1984, Hanski et al. 1993). One possible way to discern between theories is to compare frequency distributions of species occupancy to those predicted under different models (Collins and Glenn 1991, Mehranvar and Jackson 2001). Other studies have attempted to identify trait correlates of range size (Kelly and Woodward 1996, Thompson et al. 1998, Laube et al. 2013). Though there is some indication that dispersal traits can be affiliated with occupancy or extent of range (Lester et al. 2007, Laube et al. 2013), and that dispersal traits affect range of plants in particular, many factors affect range in addition to dispersal, so there is little consistency in results of different studies (Kelly and Woodward 1996, Murray et al. 2002, Ozinga et al. 2005, Siefert et al. 2015). I am not aware of any studies that investigate the relationships between plant dispersal traits and biogeographic affinity. In an era of rapid climate change, plants are particularly susceptible to local extinction because they are sessile and may take several or more generations to track shifts in location of appropriate habitat. Understanding how dispersal processes factor into the geographic range of plant species will help identify which species are most vulnerable to extinction, and is of utmost importance for both local and regional conservation of biodiversity.

Here, I analyze the relationship between dispersal morphology, range extent, frequency at a variety of spatial scales, and biogeographic affinity to give insight into the effects of spatial and temporal dispersal processes on the species composition of cove hardwood forests of the southern Appalachian Mountains. First, correlating dispersal morphology to range extent may elucidate whether local and/or long-distance dispersal influence range size, though many other processes affect range extent in addition to dispersal (Oakwood et al. 1993, Lavergne et al. 2004, Lester et al. 2007). Second, patterns of occupancy may reveal whether dispersal morphology influences frequency across the landscape, particularly if dispersal is relatively more important at

large spatial scales (Matlack 2005, Ozinga et al. 2005, Ricklefs 2008, Gove et al. 2009). Third, because the positive relationship between local abundance and occupancy can be generated by colonization and extinction dynamics between local populations, resulting in a bimodal frequency distribution of occupancy (core-satellite hypothesis, Hanski 1982), comparison of frequency distributions may indicate whether dispersal processes play a major role in structuring range-wide occurrences (Collins and Glenn 1991, Mehranvar and Jackson 2001, Murphy et al. 2006). A positive relationship between abundance and occupancy is expected for organisms structured as metapopulations, but not for dispersal limited species (Freckleton et al. 2005), and dispersal limited taxa are more likely to have an occupancy distribution weighted towards infrequent species (Mehranvar and Jackson 2001). Finally, because geographic ranges of entire lineages are affected by dispersal and vicariance, examination of the relationships between biogeographic affinity, current range, and traits including dispersal morphology may give insight into the role of dispersal in assembling regional floras (White 1983, Weakley 2005).

I hypothesized that 1) dispersal limited taxa have both lower occupancy and range extent than taxa with adaptations to wind or vertebrate dispersal; 2) taxa with dispersal assisted by wind or vertebrates are more likely to belong to widespread North Temperate or Tertiary disjunct lineages than species with unassisted dispersal; and 3) differences between dispersal categories in occupancy are stronger at larger sampling scales. Though it is difficult in this framework to demonstrate a causal relationship between process and pattern, I nevertheless examine a multitude of patterns in attempt to reveal broad scale trends that may demonstrate the importance of dispersal even in the presence of many interacting ecological factors.

Methods

Vegetation

To characterize the species composition of mesophytic coves of the southern Appalachian Mountains at several scales, I sampled rich cove vegetation in the Great Smoky Mountains National Park in three nested scales of 1 hectare, 1000 m² plots, and 100 m² modules. I targeted sample locations based on primary mesophytic community types indicated in Appendix 1 using the vegetation map of Madden et al. (2004). Each hectare had two 1000 m² plots, and each plot had 4 intensively sampled 100 m² modules. All vascular plants were identified to species or variety if possible. Cover for each species at the two smaller sampling scales was estimated using the protocol in Peet et al. (1998). This resulted in a dataset of 47 hectares and a total of 396 species, 374 of which were native and identified sufficiently precisely for analyses (Appendix 2).

Dispersal

All native plant species were assigned to nine dispersal categories based on propagule morphology. Species with adaptations for ant-dispersal have appendages (elaiosomes) to attract ants to move seeds to their nests, but this adaptation generally doesn't move propagules more than 1 meter on average, so is probably more an adaptation to germination in suitable microenvironments (Beattie and Culver 1981, Cain et al. 1998). Other species are dispersed by vertebrates, either by providing edible fruits where seeds can pass through digestive systems (endozoochory) or by attaching to the fur of passing animals using prickles, awns or other mechanical adaptations (epizoochory). In addition, many rodents and some birds hoard nuts in caches for storage, and though most seeds are destroyed when eaten, some remain viable when unrecovered. Dispersal by wind can be facilitated by winged attachments, or by seeds or fruit

with plumed appendages that allow them float through the air. Other plants have seeds so tiny (<1 mm) and light they can be dispersed by wind without specialized structures, and others, such as ferns, produce no seeds at all but reproduce by microscopic spores. Many of these dispersal mechanisms are adaptations to living in particular habitats that vary in temporal dynamics or availability of dispersal agents and in response to plant habit. Conversely, having no morphological adaptation to dispersal may be an advantage in spatially isolated optimal habitats that are temporally stable (van der Pijl 1969). Indeed, more taxa of mesophytic coxes have no obvious dispersal mechanism than are in any other dispersal category. In addition to these nine specific dispersal categories, I grouped taxa into three broader categories to evaluate similarities in dispersal distance based on general mechanisms. Wind dispersed taxa included those with wings, plumes, tiny seeds, or spores, whereas vertebrate dispersed taxa included those with propagules adapted to endozoochory, epiozoochory, or hoarding. Locally dispersed taxa either had no morphological dispersal adaptations or elaiosomes for ant dispersal.

Other traits

Many traits are correlated with dispersal morphology as a result of their evolutionary history and the ecological conditions to which they are adapted. For instance, winged seeds are most common among trees as an adaptation that allows propagules to glide away from the parent plant when released from heights, seeds with elaiosomes are restricted to the herbaceous layer of mesophytic forests, and endozoochory is common in the understory where there is an abundance of animal activity. To account for other ecological traits that may influence species distribution and interact with dispersal traits, I used several other categories to describe ecological traits of the flora. First, I used Raunkiaer's (1934) classification of life forms based on the location of buds during unfavorable seasons, resulting in plants being grouped into phanerophytes,

chamaephytes, hemicryptophytes, geophytes, and therophytes. I also grouped taxa based on growth form, including canopy trees, understory trees, shrubs, vines, graminoids, herbs, and cryptogams. This grouping system was further subdivided to classify herbaceous species by their shape, including categories for umbrella-shaped herbs (prominent in southern Appalachian coves), upright herbs, ascending herbs, and sessile herbs. Finally, I grouped plants based on leaf morphology, including categories for entire, serrate, and dentate simple leaves, pinnately or palmately lobed leaves, and pinnately, palmately, or ternately compound leaves.

Range

For each native species in this dataset, geographic range was characterized by exporting county occurrence data from USDA (2015), and error-checking using Kartesz (2015). For species with substantial ranges outside the United States, range extent was supplemented using location records exported from the Global Biodiversity Information Facility (<http://www.gbif.org>). As a measure of range extent for each taxon I used the 'geosphere' package in R version 3.1.2 to measure maximum great-circle distance with the Haversine formula across all native occurrences (R Development Core Team 2014, Hijmans 2015). To characterize range extent based on high endemism of the area, I categorized species as southern Appalachian endemics if their range was predominantly restricted to the southern half of the Appalachian Mountains, north to Pennsylvania, and west to Alabama. Local occupancy was characterized as the total number of occupied hectares, modules, and plots for each species.

Biogeographic affinity

A categorical measure of biogeographic affinity was assigned to each species based usually on the worldwide geographic distribution of their genera, though sometime on subgeneric sections, such as in the diverse genus *Carex*. The group used for analysis was

generally the smallest subgeneric group that is taxonomically and phylogenetically resolvable. Affinity categories follow Weakley (2005), and include categories for southeastern North American endemics (SENA); eastern North American endemics (ENA); North American endemics (NoAm); taxa restricted to both North and South America (Americas); taxa found worldwide but largely restricted to tropical regions (Tropical); taxa displaying classic disjunctions predominantly between eastern North America and eastern Asia (but sometimes also in western North America, the Mediterranean region, or the Caucasus Mountains) probably resulting from Tertiary relict distributions (Tertiary); Circumboreal or north temperate taxa (CB); and taxa with Cosmopolitan distributions (Cosmo).

Statistical analysis

Non-parametric statistics were used due to the non-normality of the abundance, occupancy, and range extent distributions. I used the Spearman ρ statistic to assess the correlations of average abundance with local and regional occupancy. I analyzed the relationships between categorical traits and geographic range and occupancy at local and regional scales using Kruskal-Wallis rank-sum tests for one-way analysis of variance. For strong relationships between traits and range, I performed pairwise post-hoc tests between groups using the PMCMR package in R (R Development Core Team 2014, Pohlert 2015). To test for relationships between two groups of categorical variables, I used chi-square contingency table analysis. Because biogeographic affinity is predominantly assigned on a generic basis, I eliminated duplicate genera with redundant dispersal mechanism and biogeographic affinity before analysis to avoid pseudoreplication. Because dispersal mechanism is related to growth form, to discern the independent effects of dispersal and other traits on range, occupancy, and

biogeographical affinity, I used permutational MANOVA and partial Mantel tests available in the R package 'vegan' (Oksanen et al. 2015).

Results

Occupancy

Occupancy was strongly correlated among the three grain sizes ($r > 0.9$, $p < 0.001$). Local occupancy showed largely bimodal distribution among all species and for each broad dispersal category, though the group composed of species with morphological adaptations for only local dispersal had proportionally greater abundance of rare species (Figure 5.1). Occupancy was significantly related to dispersal category at all scales, but pairwise post-hoc tests show that this was driven mainly by the differences between species with no adaptations to long distance dispersal and species dispersed by spores or vertebrates (Table 5.1). The differences between specific dispersal groups was strongest at plot and hectare scales, but broad dispersal categories had similar trends across all scales. Locally dispersed species have generally lower occupancy (Table 5.2, Figure 5.2). Comparison between growth forms showed that graminoids also had low occupancy, though more than 80% of the graminoids in this study had no apparent dispersal mechanism. Raunkiaer's life forms showed some occupancy differences, where phanerophytes and geophytes were more frequent than hemicryptophytes (Kruskal-Wallis $\chi^2 = 35.34$, $p < 0.001$). Permutational MANOVA showed that the effects of dispersal morphology on occupancy were still significant ($p < 0.05$) after controlling for differences in growth form or life form (data not shown).

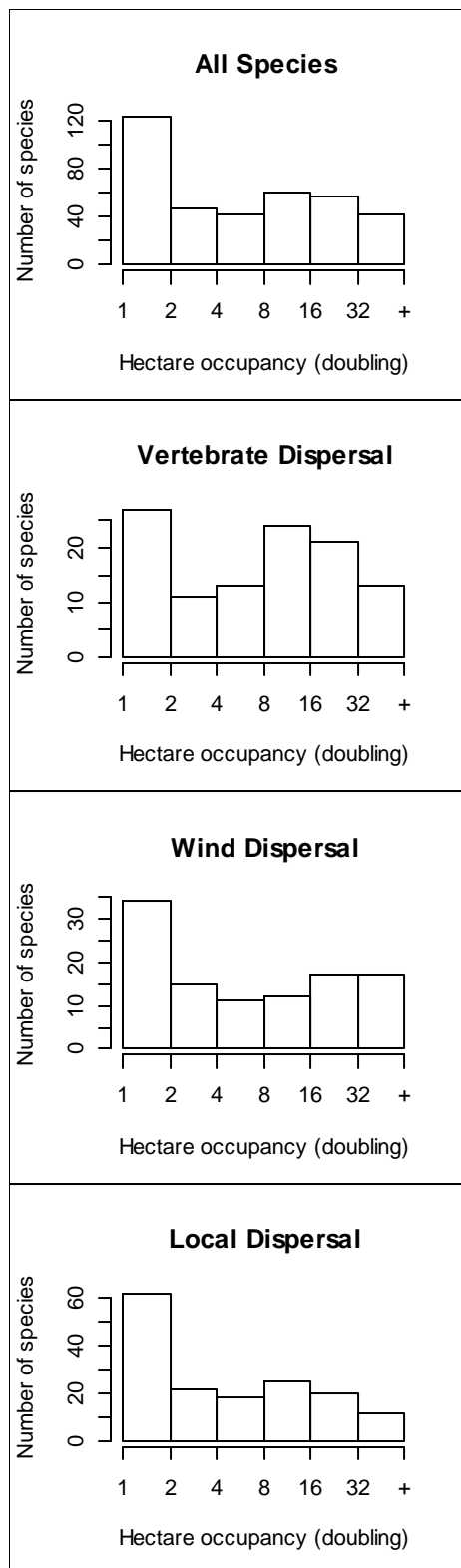


Figure 5.1. Hectare occupancy frequency distributions among all species, species dispersed by vertebrates, wind-dispersed species, and species with local dispersal.

Table 5.1. Kruskal-Wallis rank sum tests for group differences in occupancy at three grain sizes. Post-hoc comparisons show the pairwise differences that drive the relationships, with groups on either side of ~ being significantly different ($\alpha=0.05$). * $p\leq 0.05$, ** $p\leq 0.01$, *** $p\leq 0.001$.

Groups	Scale	Kruskal-Wallis χ^2	Post-hoc differences
Dispersal morphology	hectare	36.90***	none~endozoochory, spore
	plot	37.53***	none~endozoochory
	module	21.69**	
Broad dispersal groups (local, wind, vertebrate)	hectare	9.50**	local~vertebrate
	plot	10.21**	local~vertebrate
	module	9.66**	local~vertebrate
Growth form	hectare	32.28***	graminoids~trees, cryptogams, herbs
	plot	31.94***	graminoids~trees, cryptogams, herbs, vines
	module	21.92**	graminoids~trees, cryptogams, herbs

Table 5.2. Mean occupancy (hectares, plots, and modules) and range extent (maximum distance between occupied counties) for each dispersal category.

<i>Broad Group</i>	<i>Dispersal</i>	<i>n</i>	<i>Hectares</i>	<i>Plots</i>	<i>Modules</i>	<i>Range extent (km)</i>
Local	none	137	8.4	10.6	23.8	2664
	ant	21	17	23	54.3	2664
Wind	plume	27	9.5	15.1	39.6	2808
	wing	35	17.5	26.7	69.5	2550
	tiny	23	9.4	9.6	18.3	4443
	spore	22	18.4	25.6	63.4	7099
Vertebrate	hoard	15	14.5	23.1	57.7	2627
	epizoochory	30	9.8	13	27.5	3709
	endozoochory	64	15.3	20.5	42.7	2947

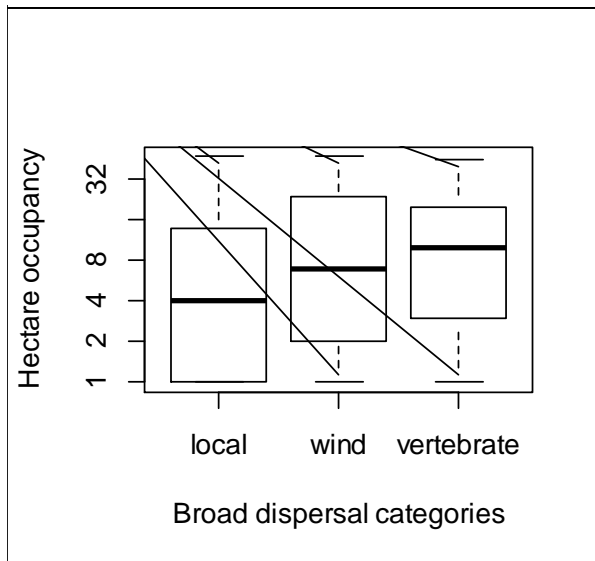


Figure 5.2. Boxplot showing local (hectare) occupancy differences between broad dispersal categories.

Range extent

Though there is substantial variation in range extent within many dispersal categories, range extent measured by maximum distance was significantly different between dispersal mechanisms (Kruskal-Wallis $\chi^2 = 26.84$ $p < 0.001$), and was driven mainly by the greater range of spore-dispersed plants as compared to species with no known dispersal mechanism (Table 5.2). Broad dispersal categories were also significantly different in range extent, with locally dispersed species having smaller ranges than either vertebrate-dispersed taxa or wind-dispersed taxa (Kruskal-Wallis $\chi^2 = 11.17$, $p < 0.01$; Table 5.2, Figure 5.3). Other than the broader range of ferns and other cryptogams (all spore-dispersed), no other plant traits or growth forms showed significant differences.

Southern Appalachian endemics composed 13% of the species analyzed in this study, and represent a nonrandom selection among species traits. Species with no dispersal adaptations were overrepresented among southern Appalachian endemics compared to all other species ($\chi^2 = 5.6$, $p < 0.05$; 19% endemics), whereas species dispersed by vertebrates and spores were underrepresented (7% and 0%, respectively). Among growth forms, herbs and shrubs were overrepresented among southern Appalachian endemics ($\chi^2 = 13.45$, $p < 0.05$; 16% and 26% endemics respectively). Leaf morphology was also strongly related to southern Appalachian endemism, where ternately compound and serrate leaves are overrepresented among endemics ($\chi^2 = 27.28$, $p < 0.001$; 33% and 28% endemics respectively). Many of these traits are correlated with each other (data not shown).

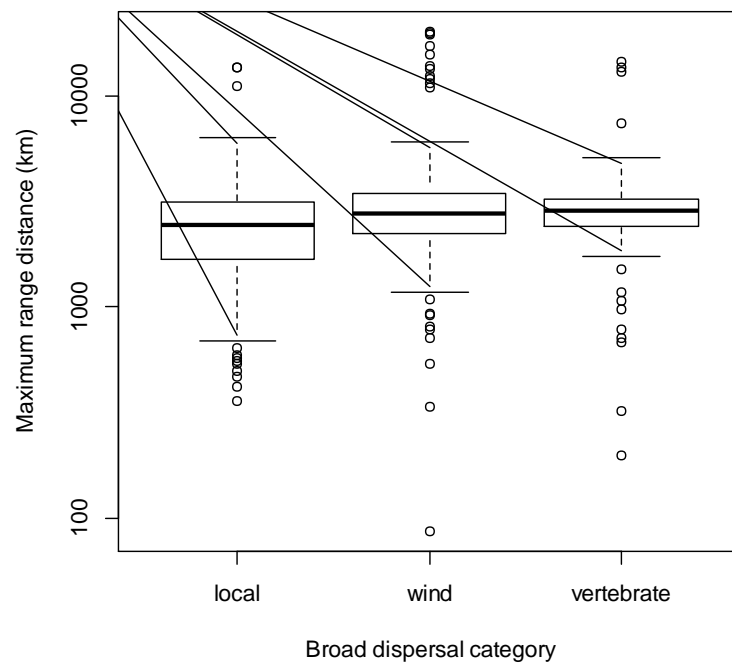


Figure 5.3. Boxplots showing differences in distribution of maximum dispersal distances among broad dispersal categories.

Biogeographic affinity

Unsurprisingly, members of widespread lineages have larger range extent than North American endemic lineages (Kruskal-Wallis $\chi^2=32.92$, $p<0.001$; Table 3). The exception to this general trend is the intermediate average range size of Tertiary disjuncts, 17% of which are southern Appalachian endemics. Biogeographic affinity was strongly related to occupancy at all spatial scales, where taxa of Tertiary disjunct lineages were most frequent (at hectare scale, Kruskal-Wallis $\chi^2=31.48$, $p<0.001$; Table 5.3). Dispersal traits are nonrandomly distributed among biogeographic affinities, where endozoochorous species are dramatically overrepresented among Tertiary disjuncts, and species with no dispersal mechanism are underrepresented ($\chi^2=91.14$, $p<0.01$, Table 5.4). Other trends are that plumed species are most likely to be from the Americas, taxa of circumboreal lineages are disproportionately winged, spore-dispersed species are most likely to be of cosmopolitan affinities, and species with no dispersal adaptations are most likely to be in lineages endemic to North America. Analysis of the distribution of other traits across biogeographic affinities reveals patterns in evolutionary history, for instance that umbrella-shaped herbs and shrubs are disproportionately of Tertiary disjunct affinities, graminoids are overrepresented in American lineages, and trees are overrepresented among Tertiary disjunct and circumboreal lineages. Many of these traits are correlated also with dispersal traits, including that graminoids and herbs frequently have only local dispersal, that trees are often dispersed by winged propagules or hoarded fruits, and that shrubs and small trees are often dispersed by endozoochory (data not shown). Despite this, partial Mantel tests showed that the effect of dispersal morphology on biogeographic affinity when controlling for growth form was weak but significant (Mantel $R=0.027$, $p<0.01$), but that growth form had no influence on biogeographic affinity independent of dispersal mechanism.

Table 5.3. Mean occupancy and range extent across taxa grouped by biogeographic affinity. *SENA*= southeastern North American endemic; *ENA*= eastern North American endemic; *NoAm*=North American endemic; *Tropical*=globally widespread but predominantly tropical taxa; *Americas*= restricted to North and South America; *Tertiary*= taxa of Tertiary disjunct affinities; primarily restricted to eastern North America and eastern Asia; *CB*= circumboreal or widespread North temperate; *Cosmo*= cosmopolitan.

<i>Affinity</i>	<i>n</i>	<i>Hectares</i>	<i>Plots</i>	<i>Modules</i>	<i>Range extent (km)</i>
<i>SENA</i>	12	9.2	9.3	16.8	1817
<i>ENA</i>	37	9.3	11.8	27.8	2049
<i>NoAm</i>	41	8.2	11.3	26.1	2378
<i>Americas</i>	10	2.4	2.7	4.1	3601
<i>Tropical</i>	10	6.5	8.6	18.7	2625
<i>Tertiary</i>	89	17.2	24.9	60.0	3123
<i>NTemp</i>	91	12.2	16.3	37.2	3585
<i>Cosmo</i>	84	11.6	15.3	34.8	3804

Table 5.4. Standardized residuals from χ^2 contingency table of dispersal mechanism and biogeographic affinity. Abbreviations of biogeographic affinity as in Table 5.3.

<i>Dispersal mechanism</i>	SENA	ENA	NoAm	Americas	Tropical	Tertiary	NTemp	Cosmo
none	-0.91	2.01	2.08	1.28	-2.28	-2.80	-0.42	1.97
ant	-0.74	0.87	-1.00	-0.51	0.75	-0.30	-0.01	0.55
plume	1.75	1.31	1.79	3.04	1.75	-2.06	-2.40	-0.02
wing	0.80	-1.18	-0.87	-0.83	-0.19	0.72	2.15	-1.76
tiny	1.55	-0.59	0.62	-0.64	1.55	-0.10	-0.29	-0.88
spore	-0.91	-1.43	-1.25	-0.64	0.32	0.44	0.27	1.62
hoard	-0.60	-0.93	0.56	-0.42	-0.60	0.55	1.65	-1.39
epizoochory	-0.89	-1.38	-1.21	-0.62	1.65	0.06	1.00	0.50
endozoochory	0.16	-0.09	-1.44	-1.06	-0.68	3.80	-1.17	-1.42

Discussion

Multiple trends in geographic range relationships support the hypothesis that dispersal processes contribute to the local, regional, and biogeographic patterns in the distribution of plants of southern Appalachian mesophytic coves. First, a bimodal occupancy distribution suggests that many plants are structured as metapopulations, a prediction of the core-satellite hypothesis based on colonization and extinction dynamics. Second, species with no dispersal adaptations have lower occupancy than species with adaptations for long distance dispersal. Third, locally-dispersed plants have smaller range extent than either wind-dispersed or vertebrate-dispersed taxa, and were more likely to be southern Appalachian endemics. Finally, analysis of biogeographic affinities shows that taxa of Tertiary disjunct affinities are more likely to be dispersed by endozoochory, while higher taxa endemic to North America are more likely to have no morphological adaptations to dispersal.

A bimodal occupancy distribution can indicate metapopulation structure at local scales (Hanski 1982, Mehranvar and Jackson 2001), while a unimodal relationship at regional scales can be indicative of a range driven by niche-filling (Brown 1995, Gaston and Blackburn 2000). In southern Appalachian coves, the bimodal pattern was observed, though many macroecological patterns can have multiple explanations. It is therefore more informative to compare patterns among species with different traits, rather than to merely confirm that the pattern exists. The bimodal distribution is most prominent among vertebrate dispersed species, whereas locally dispersed species have a higher proportion of low-occupancy species and a lower proportion of high occupancy species (Figure 5.1). These observations are in accordance with observations of Mehranvar and Jackson (2001), suggesting that dispersal limited species have occupancy distributions weighted towards rare species. Occupancy patterns at all spatial scales show that

species with no dispersal adaptations are generally more restricted in distribution than species dispersed by spores or endozoochory, and that these differences were most apparent at larger spatial scales.

Differences between dispersal mechanisms in range extent are less clear than differences in occupancy. The species dispersed by spores had the broadest range extent by far (Table 3), a trend largely driven by species disjunct between eastern North America and eastern Asia (*Onoclea sensibilis*, *Osmunda claytoniana*, *Osmundastrum cinnamomeum*, *Huperzia lucidula*), or cosmopolitan species (*Botrypus virginiana*, *Asplenium trichomanes*, *Asplenium platyneuron*). Whether this trend is truly caused by the high colonization ability of spores is unclear, because all are from very old lineages indeed, with fossil and genetic evidence showing leptosporangiate ferns dating back to the early Carboniferous, *Osmunda* being in morphological stasis since at least the early Jurassic, and *Huperzia* diverging from other lycopsids at least 200 million years ago. This suggests that some distributions could have been attained before the breakup of Pangaea by the mid-Cretaceous (Willis and McElwain 2014, Metzgar et al. 2008, Weakley 2015). The unique distribution of *Asplenium platyneuron*, which is disjunct between North America and South Africa, however, suggests that long-distance dispersal contributes to the broad geographic range of some spore-dispersed species. Long-distance dispersal is also implicated by the latitudinal patterns of geographic ranges and rate of northward recolonization after Pleistocene glaciations eliminated all flora of eastern North America north of Ohio and Pennsylvania. Despite the limited dispersal capacity among certain groups of plants, rare long-distance dispersal events are implicated in faster than expected post-glacial colonization in North America (Cain et al. 1998, Clark et al. 1998), potentially explaining the lack of strong differences in range extent among seed plants differing in dispersal morphology. Other studies

on the relationship between dispersal and range extent in plants found no clear relationship, likely owing to the many other factors that affect range size (Kelly and Woodward 1998, Gove et al. 2009).

Species with no adaptations to dispersal were overrepresented among southern Appalachian endemics, a trend that suggests either that paleoendemics that were forced south along the Appalachians during glaciations failed to recolonize northward after glacial retreat, or that neoendemics recently diverged due to population isolation in the topographically heterogeneous southern Appalachians. Research into the distribution of the closest relatives and age of divergence of endemic taxa helps discern paleoendemics from neoendemics, and suggests that dispersal limited taxa of the southern Appalachians are more commonly neoendemics due to the presence of many related species in eastern North America (e.g. *Carex austrocaroliniana*, *Pycnanthemum montanum*, *Chelone lyonii*, *Phlox stolonifera*, *Thalictrum hepaticum*). Nearly one third of southern Appalachian endemics are of Tertiary disjunct affinity, and multiple taxa are hypothesized to be paleoendemics if their closest relatives are geographically disjunct (e.g. *Astilbe biternata*, *Actaea podocarpa*, *Magnolia fraseri*, *Pyrularia pubera*, *Diphylleia cymosa*), though many of these are dispersed by vertebrates. Another interesting trend among southern Appalachian endemics is that their leaf morphology is disproportionately ternately compound (e.g. *Angelica*, *Astilbe*, *Aruncus*, *Thalictrum*, *Zizia*), a common trait convergence for herbs of mesophytic habitats (Weakley 2015). It is possible that ternately compound leaves are an adaptation to capture dappled sunlight in the understory of a lush forest, and that the regional isolation of mesophytic forests in coves of the southern Appalachians has resulted in a high proportion of endemics among species with highly divided leaves.

On broad geologic time scales, correlation between traits and biogeographic affinity reflect the evolutionary history of our flora. Because dispersal morphology is related both to growth form and evolutionary history of a lineage, it is difficult to come to definitive conclusions on the role of dispersal per se in the assembly of regional floras. However, analysis of the relationship between biogeographic affinities and dispersal morphology in combination with other traits suggests some interesting trends in the evolution and distribution of dispersal traits. It is unsurprising that many dispersal adaptations are correlated to the spatial and temporal dynamics of the environments in which the plants evolved (e.g. plumed fruits and seeds are common in open areas with abundant wind and frequent disturbance; edible fruits are common where vertebrates are abundant; local dispersal is common in stable forests where long distance dispersal could be costly to maintenance of local populations). These dispersal adaptations may be related to the biogeographic history of the northern hemisphere Tertiary, as mesophytic forests were widespread during the middle Tertiary, but cooling and drying in central and western North America contributed to the rise of grasslands and deserts in which wind-dispersed species are common (Cain et al. 1998, Graham 1999). Ecologically, then, because of the stability and historical connectivity among the mesophytic forests of eastern North America and eastern Asia, it is not unreasonable to expect that among the many shared genera of the two regions, that they should share many taxa with limited dispersal capability. However, localized dispersal is underrepresented among Tertiary disjunct taxa, while endozoochory is dramatically overrepresented. This suggests that despite the long history of mesophytic forests, taxa with limited dispersal capacity were not as likely to be exchanged between continents as those that were ingested by vertebrates, though some of ancestral taxa might have arisen from times when the the North American and Eurasian continents were connected, with descendent taxa separated

by continental drift. It is also possible that some of the taxa with limited dispersal did not enter our flora until fairly recently, are recent adaptations to persistence in stable but increasingly isolated habitats, and are more likely to be restricted to North America. The environmental changes of the later Tertiary are reflected in biogeographic affinities of plumed seeds or fruit, represented mainly by the large family Asteraceae, which is particularly prominent in open, arid vegetation. The drying of the continental interior in the late Tertiary would have brought aridland vegetation into closer proximity to the remaining mesophytic forests only fairly recently, suggesting that these taxa are a relatively late addition to our flora, rising to prominence after the closure of the Beringian and North Atlantic land bridges, thus accounting for their underrepresentation in Tertiary disjunct lineages and overrepresentation in American endemic lineages (Singh 1988, Graham 1999). The floristic history of mesophytic forests is also reflected in the compound relationship between biogeographic affinity, growth form, and dispersal. For instance, mesophytic forest trees, predominantly dispersed by winged seeds or cached nuts, often are of circumboreal or Tertiary disjunct affinity, a relic of the widespread mesophytic forests of the mid-Tertiary and disproportionate extinction in Europe and western North America from later Tertiary to Quaternary times (Gray 1878, Graham 1999). The overrepresentation of umbrella-shaped herbs among Tertiary disjunct lineages is also likely a reflection of the ecological conditions of the widespread mesophytic forests of the mid-Tertiary, and their subsequent reduction in area (Cain 1943, Whittaker 1956).

The biogeographical relationships of mesophytic forests of the southern Appalachians have been linked many times with Tertiary history and the disjunction between eastern North America and eastern Asia (Cain 1943, Whittaker 1956). In particular, previous studies have shown that taxa of Tertiary disjunction are particularly common in mesic habitats, most likely of

primitive lineages, disproportionately woody, and large contributors to southern Appalachian endemism (White 1983, Weakley 2005). The results of the present study are largely consistent. In addition, this study shows that dispersal morphology is related to biogeographic affinity, particularly in the case of Tertiary relict distributions. This corresponds well to the ideas advocated by Tiffney (1975) that dispersal morphology of Tertiary angiosperms evolved in response to the ecological conditions and growth habits of the time, and that greater dispersal capacity favored the intercontinental allopatric speciation that is manifested in the eastern North American-eastern Asian disjunction.

The difficulty in discerning the role of dispersal in affecting biogeographic distributions is that dispersal traits are correlated with many other traits and with the entire history of mesophytic forests. Part of this is due to niche conservatism, because leaf morphology, growth form, and dispersal morphology are traits that tend to be conserved within lineages, but trends can also be interpreted as evolving as common adaptations to the environmental conditions of mesophytic forests (Tiffney 1984, Ricklefs and Latham 1992, Webb et al. 2002, Cavender-Bares et al. 2009). An often-suggested solution to assessing the importance of traits as opposed to phylogeny in determining distributions is to use phylogenetically independent contrasts as a null model, where species are compared directly only to other species in their lineage that vary in the trait of interest (Kelly and Woodward 1996, Gaston and Blackburn 2000, Gove et al. 2009). Unfortunately, due to the ecological and geographical limitation of this dataset, there are too few genera (5) with more than one species that vary in dispersal mechanism, so phylogenetically independent contrasts are not possible. Those studies that have used phylogenetically independent contrasts are inconclusive, and suggest that many other factors contribute to range size (Kelly and Woodward 1996, Gove et al. 2009).

Despite the challenges in isolating the role of dispersal from other traits influencing the ranges of plant species, this study suggests that dispersal is a process integral to both local and regional biogeographic distributions. Rather than being separate from ecological interactions, dispersal interacts with local conditions to influence local population dynamics as well as regional processes of speciation and extinction. At landscape and regional scales, species without dispersal adaptations tend to have lower occupancy despite similar habitat preference. Over longer time scales, changes in the distribution and abundance of habitats interact with dispersal processes, causing spatial isolation, speciation, relictual distributions, and differing patterns of endemism between species with different dispersal mechanisms (Cain 1944, Delcourt and Delcourt 1975, Graham 1999, Soltis et al. 2006, Gonzalez et al. 2008). The relationships between dispersal traits, range, occupancy, and biogeographic affinity demonstrated in this study emerged over a long period of time as an indication of the entire distributional history of the mixed mesophytic forest, and reflect the evolutionary history of each individual taxon as well as the composite changes of the flora (Graham 1999). Future research should combine area cladograms of individual taxa with dispersal adaptations and ecological conditions (Arbogast and Kenagy 2001, Donoghue and Moore 2003), in order to evaluate whether differences in dispersal ability affect patterns of distribution of higher level taxa. Analysis of the conservation of dispersal and ecological traits and divergence timing within lineages will elucidate whether species without dispersal adaptations are more restricted in distribution because of limited dispersal or because they are more recent additions to our flora (Donoghue 2008, Cavender-Bares et al. 2009). It may also help us understand the role historical dispersal plays in the evolution and geographical distribution of paleoendemics and neoendemics (Harshberger 1911, Cain 1944, Graham and Fine 2008).

This study paints a comprehensive picture of the complex history of the mesophytic flora of the southern Appalachian Mountains, and indicates that contemporary and historical dispersal processes in the context of ecological interactions affect species distributions across many scales of space and time. In the contemporary context of rapidly changing climate and habitat destruction, this study suggests that dispersal limited plant species are at increased risk of local and regional extinction, and that dispersal processes should be accounted for in efforts to conserve plant biodiversity. Though the results shown here are system-specific and trends will likely vary in other regions with different climatic, evolutionary, and biogeographic history, the approach may be applied to other areas to assess the role of dispersal in assembling regional species pools and affecting regional species distributions.

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CHAPTER 6. SYNTHESIS AND CONCLUSIONS

The flora of mesophytic forests in the southern Appalachian Mountains has been, and continues to be, shaped by the interaction of dispersal processes with environmental heterogeneity across several scales of space and time. This study demonstrates the importance of dispersal to plant species distribution and diversity, not just at regional and biogeographic scales, but also at landscape, habitat, and neighborhood scales. The focus on mixed mesophytic forests was, in part, personal, but was also functional, in that it was designed to minimize effects of the strong environmental gradients of the Smoky Mountains from overwhelming any signal of dispersal. In addition, the mixed mesophytic forest turned out to be the ideal study system because it has high species richness and displays several levels of habitat connectivity.

The importance of dispersal in this study was assessed through comparison between species groups based on differences in dispersal morphology, and through use of spatial predictors representing dispersal processes independently of environmental gradients at a variety of scales. These predictors included measures of habitat connectivity, and were incorporated into models of species and communities, indicating that even though environmental conditions are strong predictors of observed patterns in species and communities, spatial processes including dispersal are important determinants of species distributions and community composition.

At neighborhood and habitat scales, many species were clumped, due in part to dispersal limitation, and accounting for presence in nearby locations and habitat connectivity helped predict occurrence even after environmental variables were accounted for. At landscape scales,

distribution models for dispersal-limited species were most dramatically improved by the inclusion of spatial predictors as compared to wind or vertebrate dispersed plants.

At habitat and landscape scales, the greater proportion of rare species among plants adapted for only local dispersal contributed to spatially nonrandom co-occurrence patterns. Spatial predictors affected nonrandom patterns of species turnover independently of environmental predictors, and more strongly for locally dispersed species than for wind- or vertebrate-dispersed species.

At landscape and regional scales, dispersal limited plants were less frequent and had a broader geographic range than wind-dispersed or vertebrate-dispersed plants. They were also more likely to be southern Appalachian endemics. And at biogeographical scales, dispersal morphology reflects biogeographic history, where plants of Tertiary disjunct lineages are far more likely to be dispersed by endozoochory, and taxa with no obvious dispersal adaptations are more likely to be in lineages endemic to North America. The extensive biogeographic history of members of mixed mesophytic forests dates back to the Tertiary period, when many taxa were widespread across the northern hemisphere owing to geographic and climatic connections between North America and Eurasia. Since then, as mixed mesophytic forests have grown more isolated, particularly in the southern Appalachian Mountains, the flora has continued to change and evolve, with many higher-level taxa endemic to North America, as well as many species endemic to the southern Appalachians.

Because methods differ between analyses at different scales, it is difficult to definitively answer the question of whether dispersal processes are more important at broader scales. It certainly seems the case that differences between dispersal categories are more apparent at regional and biogeographical scales than at neighborhood and habitat scales. However, the

results shown here indicate that spatial processes including dispersal affect species distribution and community composition even at relatively small scales, so it would be inappropriate to assume that the effects of dispersal limitation are negligible at any scale.

APPENDIX 1. PRIMARY AND SECONDARY COMMUNITY TYPES FOR TARGETING OF SAMPLE AREAS AND ASSIGNING NETWORK CONNECTIVITY

Community names were associated between Schafale 2012 and the National Vegetation Classification (NVC) using Community Element Global (CEGL) codes. Primary and secondary rank communities were chosen using community descriptions in Schafale 2012, Schafale and Weakley 1990, White et al. 2003, and NatureServe 2015.

<i>Schafale 2012 Name</i>	<i>NVC Name</i>	<i>CEGL</i>	<i>Rank</i>
Rich Cove Forest (Montane Rich Subtype)	Southern Appalachian Rich Cove Forest (Montane Calcareous Type)	7695	Primary
Rich Cove Forest (Montane Intermediate Subtype)	Southern Appalachian Rich Cove Forest (Typic Montane Type)	7710	Primary
Rich Cove Forest (Red Oak Subtype)	Southern Appalachian Red Oak Cove Forest	7878	Primary
Rich Cove Forest (Boulderfield Subtype)	Southern Appalachian Hardwood Rich Boulderfield Forest	4982	Primary
Northern Hardwood Forest (Rich Subtype)	Southern Appalachian Northern Hardwood Forest (Rich Type)	4973	Primary
Northern Hardwood Forest (Typic Subtype)	Southern Appalachian Northern Hardwood Forest (Typic Type)	7285	Primary
Northern Hardwood Forest (Beech Gap Subtype)	Southern Appalachian Beech Gap	6130	Primary
High Elevation Birch Boulderfield Forest	Southern Appalachian Boulderfield Forest (Currant and Rockcap Fern Type)	6124	Primary
High Elevation Red Oak Forest (Typic Herb Subtype)	High-Elevation Red Oak Forest (Deciduous Shrub Type)	7300	Secondary
Low Montane Red Oak Forest	Appalachian Montane Oak-Hickory Forest (Red Oak Type)	6192	Secondary
Montane Oak-Hickory Forest (Basic Subtype)	Appalachian Montane Oak-Hickory Forest (Rich Type)	7692	Primary
Montane Oak-Hickory Forest (White Pine Subtype)	Appalachian White Pine - Mesic Oak Forest	7517	Secondary
Canada Hemlock Forest (White Pine Subtype)	Southern Appalachian Eastern Hemlock Forest (White Pine Type)	7102	Secondary
Canada Hemlock Forest (Typic Subtype)	Southern Appalachian Eastern Hemlock Forest (Typic Type)	7136	Secondary
Acidic Cove Forest (Typic Subtype)	Southern Appalachian Acid Cove Forest (Typic Type)	7543	Secondary
Acidic Cove Forest (Silverbell Subtype)	Southern Appalachian Acid Cove Forest (Silverbell Type)	7693	Secondary
Acidic Cove Forest (High Elevation Subtype)	Blue Ridge Hemlock-Northern Hardwood Forest	7861	Secondary
Rich Montane Seep	Rich Montane Seep (High Elevation Type)	4293	Primary
Rich Montane Seep	Rich Montane Seep (Cove Type)	4296	Primary
Montane Alluvial Forest (Large River Subtype)	Appalachian Montane Alluvial Forest	4691	Primary
Montane Alluvial Forest (Small River Subtype)	Southern Appalachian Small River Floodplain Forest	7143	Primary
	Southern Appalachian Mixed Hardwood Forest	8558	Secondary
	Early Successional Appalachian Hardwood Forest	7219	Secondary
	Successional Black Walnut Forest	7879	Secondary

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APPENDIX 2. FULL SPECIES LIST

* Species used as indicators for targeting mixed mesophytic areas. Taken from Schafale and Weakley 1990, Ulrey 2002, Schafale 2012, NatureServe 2015, Weakley 2015, and White et al. 2003.

† Indicates taxa that are endemic to the central and southern Appalachian Mountains
Analysis unit lists the species used for biogeographical analyses if different than recorded taxon.
NA= not applicable/not analyzed.

Dispersal vector is based on external seed, fruit, or spore size and morphology.

Biogeographical affinity and group adapted from Weakley 2005. Americas = widespread throughout the new world; NT=widespread north temperate; Cosmo = cosmopolitan; ENA = eastern North American endemic; Tertiary= Tertiary relictual taxa primarily distributed in eastern North America and eastern Asia but sometimes also including taxa in western North America, Caucasus Mountains, and the Mediterranean; NoAm = endemic to North America; SENA= southeastern North American endemic; Tropical = widespread but low latitudes.

Species	Analysis unit	Dispersal	Affinity	Biogeographical group
<i>Acer pensylvanicum</i> *		wing	Tertiary	section
<i>Acer rubrum</i>		wing	Tertiary	section
<i>Acer saccharum</i> *		wing	NTemp	section
<i>Acer spicatum</i> *		wing	Tertiary	section
<i>Actaea pachypoda</i> *		endozoochory	Tertiary	genus
<i>Actaea podocarpa</i> *†		none	Tertiary	genus
<i>Actaea racemosa</i> *		none	Tertiary	genus
<i>Adiantum pedatum</i> *		spore	Cosmo	genus
<i>Aesculus flava</i> *†		hoard	Tertiary	genus
<i>Ageratina altissima</i> *		plume	Tropical	genus
<i>Agrimonia gryposepala</i>		epizoochory	NTemp	genus
<i>Agrimonia parviflora</i>		epizoochory	NTemp	genus
<i>Agrimonia rostellata</i>		epizoochory	NTemp	genus
<i>Agrostis</i>	NA	none	NTemp	genus
<i>Allium tricoccum</i> *		none	NTemp	genus
<i>Ambrosia artemisiifolia</i>		none	Cosmo	genus
<i>Ambrosia trifida</i>		none	Cosmo	genus
<i>Amelanchier arborea</i>		endozoochory	NTemp	genus
<i>Amelanchier laevis</i>		endozoochory	NTemp	genus
<i>Amphicarpaea bracteata</i>		none	Tertiary	genus
<i>Anemone acutiloba</i> *		ant	NTemp	section
<i>Anemone quinquefolia</i> *		ant	Cosmo	section
<i>Anemone virginiana</i>		plume	Cosmo	section

<i>Angelica triquinata</i> *†		wing	NTemp	genus
<i>Aquilegia canadensis</i> *		none	NTemp	genus
<i>Aralia nudicaulis</i>		endozoochory	Tertiary	genus
<i>Aralia racemosa</i> *		endozoochory	Tertiary	genus
<i>Aralia spinosa</i>		endozoochory	Tertiary	genus
<i>Arisaema dracontium</i>		endozoochory	Tertiary	genus
<i>Arisaema triphyllum</i>		endozoochory	Tertiary	genus
<i>Arnoglossum reniforme</i> *		plume	ENA	genus
<i>Aruncus dioicus</i> var. <i>dioicus</i> *†		none	NTemp	genus
<i>Arundinaria gigantea</i>		none	SENA	genus
<i>Asarum canadense</i> *		ant	Tertiary	section
<i>Asclepias exaltata</i>		plume	Americas	genus
<i>Asclepias variegata</i>		plume	Americas	genus
<i>Asclepias verticillata</i>		plume	Americas	genus
<i>Asimina triloba</i> *		endozoochory	ENA	genus
<i>Asplenium platyneuron</i>		spore	Cosmo	genus
<i>Asplenium rhizophyllum</i> *		spore	Tertiary	section
<i>Asplenium trichomanes</i>		spore	Cosmo	genus
<i>Asteraceae</i>	NA	plume	unknown	unknown
<i>Astilbe biternata</i> *†		none	Tertiary	genus
<i>Athyrium asplenioides</i>		spore	NTemp	genus
<i>Betula alleghaniensis</i> *		wing	NTemp	genus
<i>Betula lenta</i> var. <i>lenta</i> *		wing	NTemp	genus
<i>Bignonia capreolata</i>		wing	SENA	genus
<i>Boechera laevigata</i>		none	NTemp	genus
<i>Boehmeria cylindrica</i>		none	Cosmo	genus
<i>Botrypus virginianus</i> *		spore	NTemp	genus
<i>Brachyelytrum erectum</i> *		epizoochory	Tertiary	genus
<i>Bromus pubescens</i>		epizoochory	NTemp	genus
<i>Calycanthus floridus</i> †		none	NoAm	genus
<i>Campanula divaricata</i> †		none	Cosmo	genus
<i>Campanulastrum americanum</i>		none	ENA	genus
<i>Cardamine diphylla</i> *		ant	Cosmo	genus
<i>Carex aestivalis</i>		none	Cosmo	section
<i>Carex albicans</i>		none	NTemp	section
<i>Carex albursina</i> *		none	NoAm	section
<i>Carex allegheniensis</i>		none	Cosmo	section
<i>Carex amphibola</i>		none	NoAm	section
<i>Carex appalachica</i> *		none	NoAm	section
<i>Carex austrocaroliniana</i> *†		none	ENA	section
<i>Carex bromoides</i>		none	Tertiary	section

<i>Carex cephalophora</i>		none	NoAm	section
<i>Carex cherokeensis</i> *		none	Cosmo	section
<i>Carex communis</i>		none	NTemp	section
<i>Carex cumberlandensis</i> *		none	ENA	section
<i>Carex debilis</i>		none	Cosmo	section
<i>Carex digitalis</i> var. <i>digitalis</i>	<i>Carex digitalis</i>	none	ENA	section
<i>Carex fraseri</i> *†		none	SENA	section
<i>Carex gracilescens</i> *		none	NoAm	section
<i>Carex gracillima</i>		none	Cosmo	section
<i>Carex intumescens</i> *		none	ENA	section
<i>Carex kraliana</i>		none	NoAm	section
<i>Carex laxiculmis</i> var. <i>copulata</i>		none	ENA	section
<i>Carex laxiflora</i>		none	NoAm	section
<i>Carex leptonervia</i> *		none	NoAm	section
<i>Carex manhartii</i> *†		none	NoAm	section
<i>Carex pensylvanica</i>		none	NTemp	section
<i>Carex plantaginea</i> *		none	ENA	section
<i>Carex rosea</i>		none	NoAm	section
<i>Carex scabrata</i>		none	Tertiary	section
<i>Carex styloflexa</i>		none	NoAm	section
<i>Carex torta</i>		none	Cosmo	section
<i>Carex umbellata</i>		none	NTemp	section
<i>Carex virescens</i> *		none	NTemp	section
<i>Carpinus caroliniana</i>		wing	NTemp	genus
<i>Carya cordiformis</i> *		hoard	Tertiary	genus
<i>Carya glabra</i>		hoard	Tertiary	genus
<i>Carya ovata</i> *		hoard	Tertiary	genus
<i>Carya tomentosa</i>		hoard	Tertiary	genus
<i>Castanea dentata</i>		hoard	NTemp	genus
<i>Catalpa bignonioides</i>		wing	Tertiary	genus
<i>Caulophyllum thalictroides</i> *		endozoochory	Tertiary	genus
<i>Cercis canadensis</i>		wing	Tertiary	genus
<i>Chamaecrista nictitans</i>		ant	Tropical	genus
<i>Chelone glabra</i>		none	ENA	genus
<i>Chelone lyonii</i> *†		none	ENA	genus
<i>Chimaphila maculata</i>		none	NTemp	genus
<i>Chrysosplenium americanum</i> *		none	NTemp	genus
<i>Cicuta maculata</i>		none	NTemp	<NA>
<i>Cinna latifolia</i>		none	NTemp	genus
<i>Circaea alpina</i> ssp. <i>alpina</i> *		epizoochory	NTemp	genus
<i>Circaea canadensis</i> ssp. <i>canadensis</i> *		epizoochory	NTemp	genus

<i>Cladrastis kentukea</i> *		wing	Tertiary	genus
<i>Clematis virginiana</i>		wing	Cosmo	subgenus
<i>Clethra acuminata</i> †		tiny	Tropical	genus
<i>Clintonia umbellulata</i> *		endozoochory	Tertiary	genus
<i>Collinsonia canadensis</i> *		none	ENA	genus
<i>Conoclinium coelestinum</i>		plume	NoAm	genus
<i>Conopholis americana</i>		endozoochory	NoAm	genus
<i>Convallaria majuscula</i> †		endozoochory	NTemp	genus
<i>Cornus alternifolia</i> *		endozoochory	Tertiary	subgenus
<i>Cornus florida</i>		endozoochory	Tertiary	subgenus
<i>Corylus americana</i>		hoard	NTemp	genus
<i>Crataegus</i>	NA	endozoochory	NTemp	genus
<i>Cryptotaenia canadensis</i>		none	Tertiary	genus
<i>Cuscuta rostrata</i> †		none	Cosmo	genus
<i>Cypripedium parviflorum</i> *		tiny	NTemp	genus
<i>Cystopteris protrusa</i> *		spore	NTemp	genus
<i>Danthonia compressa</i>		epizoochory	NTemp	genus
<i>Delphinium tricornis</i> *		none	NTemp	genus
<i>Dennstaedtia punctilobula</i>		spore	Cosmo	genus
<i>Deparia acrostichoides</i> *		spore	Tertiary	genus
<i>Desmodium canescens</i>		epizoochory	Cosmo	genus
<i>Dichanthelium boscii</i>		none	Americas	genus
<i>Dichanthelium clandestinum</i>		none	Americas	genus
<i>Dichanthelium commutatum</i>		none	Americas	genus
<i>Dichanthelium dichotomum</i> group	<i>Dichanthelium dichotomum</i>	none	Americas	genus
<i>Dioscorea villosa</i>		wing	Tertiary	section
<i>Diphylleia cymosa</i> *†		endozoochory	Tertiary	genus
<i>Diplazium pycnocarpon</i> *		spore	Tropical	genus
<i>Dryopteris goldiana</i> *		spore	Cosmo	section
<i>Dryopteris intermedia</i> *		spore	Cosmo	genus
<i>Dryopteris marginalis</i> *		spore	Cosmo	genus
<i>Elaeagnus umbellata</i>	NA	endozoochory	nonnative	genus
<i>Elymus hystrix</i>		epizoochory	Cosmo	genus
<i>Elymus virginicus</i>		epizoochory	Cosmo	genus
<i>Epifagus virginiana</i>		none	ENA	genus
<i>Erechtites hieracifolia</i>		plume	Americas	genus
<i>Erigeron pulchellus</i>		plume	Cosmo	genus
<i>Euonymus americanus</i>		endozoochory	Cosmo	genus
<i>Euonymus obovatus</i> *†		endozoochory	Cosmo	section
<i>Eurybia [chlorolepis + divaricata]</i> *	<i>Eurybia divaricata</i>	plume	NoAm	section

<i>Eurybia macrophylla</i> *		plume	NoAm	genus
<i>Eutrochium fistulosum</i>		plume	SENA	genus
<i>Eutrochium purpureum</i>		plume	SENA	genus
<i>Eutrochium steelei</i> *†		plume	SENA	genus
<i>Fagus grandifolia</i>		hoard	NTemp	genus
<i>Festuca subverticillata</i>		none	Cosmo	genus
<i>Fraxinus americana</i>		wing	NTemp	genus
<i>Fraxinus pennsylvanica</i>		wing	NTemp	genus
<i>Galax urceolata</i> †		none	SENA	genus
<i>Galearis spectabilis</i>		tiny	Tertiary	genus
<i>Galium circaeazans</i>		epizoochory	Cosmo	genus
<i>Galium lanceolatum</i> *		epizoochory	Cosmo	genus
<i>Galium latifolium</i> †		none	Cosmo	genus
<i>Galium triflorum</i> *		epizoochory	Cosmo	genus
<i>Gaylussacia ursina</i> †		endozoochory	ENA	subgeneric clade
<i>Gentiana decora</i> †		wing	NTemp	section
<i>Geranium maculatum</i> *		none	Cosmo	genus
<i>Geum canadense</i>		epizoochory	NTemp	subgenus
<i>Geum virginianum</i>		epizoochory	NTemp	subgenus
<i>Gillenia trifoliata</i>		none	ENA	genus
<i>Glechoma hederacea</i>	NA	none	nonnative	NA
<i>Glyceria melicaria</i>		none	Cosmo	genus
<i>Glyceria striata</i>		none	Cosmo	genus
<i>Goodyera pubescens</i>		tiny	NTemp	genus
<i>Goodyera repens</i>		tiny	NTemp	genus
<i>Halesia tetraptera</i> †		wing	Tertiary	genus
<i>Hamamelis virginiana</i>		none	Tertiary	genus
<i>Hedera helix</i>	NA	endozoochory	nonnative	genus
<i>Helianthus</i>	NA	none	NoAm	genus
<i>Helianthus giganteus</i>		none	NoAm	genus
<i>Helianthus microcephalus</i>		none	NoAm	genus
<i>Helianthus strumosus</i>		none	NoAm	genus
<i>Heuchera villosa</i> †		tiny	NoAm	genus
<i>Hexastylis arifolia</i> var. <i>ruthii</i> †		ant	Tertiary	genus
<i>Houstonia purpurea</i>		tiny	ENA	genus
<i>Houstonia serpyllifolia</i> *†		tiny	ENA	genus
<i>Huperzia lucidula</i>		spore	NTemp	genus
<i>Hybanthus concolor</i> *		none	ENA	subgenus
<i>Hydaticea petiolaris</i> *†		none	NTemp	genus
<i>Hydrangea arborescens</i> *		tiny	Tertiary	genus
<i>Hydrophyllum canadense</i> *		none	NoAm	genus

<i>Hydrophyllum virginianum</i> *		none	NoAm	genus
<i>Hylodesmum glutinosum</i> *		epizoochory	Tertiary	genus
<i>Hylodesmum nudiflorum</i>		epizoochory	Tertiary	genus
<i>Hypericum</i>	NA	tiny	NTemp	genus
<i>Ilex montana</i>		endozoochory	Cosmo	genus
<i>Ilex opaca</i>		endozoochory	Cosmo	genus
<i>Impatiens capensis</i>		none	Cosmo	genus
<i>Impatiens pallida</i> *		none	Cosmo	genus
<i>Iris cristata</i> *		ant	NTemp	genus
<i>Isotrema macrophylla</i> *†		none	Tertiary	genus
<i>Juglans cinerea</i> *		hoard	Tertiary	genus
<i>Juglans nigra</i> *		hoard	Tertiary	genus
<i>Juncus effusus</i>		tiny	Cosmo	subgeneric clade
<i>Juncus tenuis</i>		tiny	Cosmo	subgeneric clade
<i>Kalmia latifolia</i>		tiny	SENA	genus
<i>Lactuca biennis</i>		plume	Cosmo	genus
<i>Laportea canadensis</i> *		none	Tertiary	genus
<i>Leersia oryzoides</i>		none	Cosmo	genus
<i>Leersia virginica</i>		none	Cosmo	genus
<i>Leucothoe fontanesiana</i> †		none	Tertiary	genus
<i>Ligusticum canadense</i> *		none	NTemp	genus
<i>Ligustrum sinense</i>	NA	endozoochory	nonnative	NA
<i>Lilium superbum</i>		wing	Tertiary	genus
<i>Lindera benzoin</i> *		endozoochory	Tertiary	genus
<i>Liquidambar styraciflua</i>		wing	Tertiary	genus
<i>Liriodendron tulipifera</i> var. <i>tulipifera</i>		wing	Tertiary	genus
<i>Lobelia cardinalis</i>		tiny	Cosmo	genus
<i>Lobelia inflata</i>		tiny	Cosmo	genus
<i>Lonicera japonica</i>	NA	endozoochory	nonnative	genus
<i>Ludwigia palustris</i>		tiny	NoAm	section
<i>Luzula acuminata</i>		ant	Cosmo	genus
<i>Lycopus uniflorus</i>		none	NTemp	genus
<i>Lyonia ligustrina</i>		none	Tertiary	genus
<i>Lysimachia nummularia</i>	NA	none	nonnative	genus
<i>Lysimachia quadrifolia</i>		none	Cosmo	genus
<i>Magnolia acuminata</i> *		endozoochory	Tertiary	section
<i>Magnolia fraseri</i> †		endozoochory	SENA	section
<i>Magnolia tripetala</i> *		endozoochory	Tertiary	section
<i>Maianthemum canadense</i>		endozoochory	NTemp	genus
<i>Maianthemum racemosum</i> ssp. <i>racemosum</i> *		endozoochory	NTemp	genus

<i>Medeola virginiana</i>		endozoochory	ENA	genus
<i>Melilotus albus</i>	NA	none	nonnative	NA
<i>Menispermum canadense</i>		endozoochory	Tertiary	genus
<i>Micranthes micranthidifolia</i> *†		none	NTemp	genus
<i>Micranthes virginensis</i>		none	NTemp	genus
<i>Microstegium vimineum</i>	NA	none	nonnative	genus
<i>Mitchella repens</i>		endozoochory	Tertiary	genus
<i>Mitella diphylla</i> *		none	Tertiary	genus
<i>Monarda clinopodia</i> *		none	NoAm	genus
<i>Monarda didyma</i> *		none	NoAm	genus
<i>Monarda media</i>		none	NoAm	genus
<i>Monotropa uniflora</i>		tiny	Tertiary	genus
<i>Muhlenbergia sobolifera</i>		none	Tertiary	genus
<i>Muhlenbergia tenuiflora</i>		none	Tertiary	genus
<i>Nabalus</i>	NA	plume	Tertiary	genus
<i>Nyssa sylvatica</i>		endozoochory	Tertiary	genus
<i>Oclemena acuminata</i>		plume	ENA	genus
<i>Onoclea sensibilis</i>		spore	Tertiary	genus
<i>Osmorhiza claytonii</i> *		epizoochory	Tertiary	genus
<i>Osmorhiza longistylis</i> *		epizoochory	Tertiary	genus
<i>Osmunda claytoniana</i> *		spore	Tertiary	genus
<i>Osmundastrum cinnamomeum</i>		spore	Tertiary	genus
<i>Ostrya virginiana</i>		wing	NTemp	genus
<i>Oxalis stricta</i>		none	Cosmo	genus
<i>Oxalis violacea</i>		none	Cosmo	genus
<i>Oxydendrum arboreum</i>		tiny	SENA	genus
<i>Panax quinquefolius</i> *		endozoochory	Tertiary	genus
<i>Parthenocissus quinquefolia</i>		endozoochory	Tertiary	genus
<i>Pedicularis canadensis</i>		none	NTemp	genus
<i>Persicaria</i>	NA	none	Cosmo	genus
<i>Persicaria sagittata</i>		none	Cosmo	genus
<i>Persicaria virginiana</i>		epizoochory	Tertiary	genus
<i>Phacelia bipinnatifida</i> *		none	NoAm	genus
<i>Phegopteris hexagonoptera</i> *		spore	NTemp	genus
<i>Philadelphus hirsutus</i> *†		none	NoAm	subgeneric clade
<i>Phlox amplifolia</i> *		none	NoAm	genus
<i>Phlox glaberrima</i>		none	NoAm	genus
<i>Phlox paniculata</i>		none	NoAm	genus
<i>Phlox stolonifera</i> *†		none	NoAm	genus
<i>Phryma leptostachya</i> *		epizoochory	Tertiary	genus
<i>Phytolacca americana</i>		endozoochory	Tropical	genus

<i>Picea rubens</i>		wing	NTemp	genus
<i>Pilea pumila</i>		wing	Cosmo	genus
<i>Pinus strobus</i>		wing	NTemp	genus
<i>Pinus virginiana</i>		wing	NTemp	genus
<i>Plantago rugelii</i>	NA	none	nonnative	genus
<i>Platanthera [grandiflora + psycodes]*</i>	<i>Platanthera psycodes</i>	tiny	NTemp	genus
<i>Platanus occidentalis</i>		plume	Tertiary	genus
<i>Poa alsodes</i> *		none	Cosmo	genus
<i>Poa cuspidata</i> †		none	Cosmo	genus
<i>Poa sylvestris</i>		none	Cosmo	genus
<i>Podophyllum peltatum</i> *		endozoochory	Tertiary	genus
<i>Polygonatum biflorum</i>		endozoochory	NTemp	genus
<i>Polygonatum pubescens</i> *		endozoochory	NTemp	genus
<i>Polymnia canadensis</i> *		none	ENA	genus
<i>Polypodium appalachianum</i> *		spore	Cosmo	genus
<i>Polystichum acrostichoides</i>		spore	Cosmo	genus
<i>Potamogeton</i>	NA	none	Cosmo	genus
<i>Potentilla canadensis</i>		none	NTemp	genus
<i>Prosartes lanuginosa</i> *		endozoochory	Tertiary	genus
<i>Prunella vulgaris</i>		none	NTemp	genus
<i>Prunus pensylvanica</i>		endozoochory	Cosmo	genus
<i>Prunus serotina</i>		endozoochory	Cosmo	genus
<i>Pycnanthemum montanum</i> *†		none	ENA	genus
<i>Pyrolaria pubera</i> †		endozoochory	Tertiary	genus
<i>Quercus alba</i>		hoard	NTemp	section
<i>Quercus imbricaria</i>		hoard	NoAm	section
<i>Quercus montana</i>		hoard	NTemp	section
<i>Quercus rubra</i> *		hoard	NoAm	section
<i>Quercus velutina</i>		hoard	NoAm	section
<i>Ranunculus abortivus</i>		none	NTemp	section
<i>Ranunculus hispidus</i>		none	Cosmo	section
<i>Ranunculus recurvatus</i>		none	Cosmo	section
<i>Reynoutria japonica</i>	NA	none	nonnative	NA
<i>Rhododendron calendulaceum</i> †		tiny	Tertiary	section
<i>Rhododendron maximum</i>		tiny	Tertiary	section
<i>Ribes cynosbati</i> *		epizoochory	NTemp	genus
<i>Robinia pseudoacacia</i>		wing	SENA	genus
<i>Rosa multiflora</i>	NA	endozoochory	nonnative	genus
<i>Rubus allegheniensis</i>		endozoochory	Cosmo	genus
<i>Rubus canadensis</i>		endozoochory	Cosmo	genus
<i>Rubus odoratus</i> *		endozoochory	Cosmo	genus

<i>Rudbeckia laciniata</i> *		none	NoAm	genus
<i>Rugelia nudicaulis</i> †		plume	SENA	genus
<i>Rumex obtusifolius</i>	NA	wing	nonnative	genus
<i>Sambucus canadensis</i>		endozoochory	NTemp	genus
<i>Sambucus racemosa</i> *		endozoochory	NTemp	genus
<i>Sanguinaria canadensis</i> *		ant	ENA	genus
<i>Sanicula canadensis</i>		epizoochory	Cosmo	genus
<i>Sanicula marilandica</i>		epizoochory	Cosmo	genus
<i>Sanicula odorata</i> *		epizoochory	Cosmo	genus
<i>Sanicula smallii</i>		epizoochory	Cosmo	genus
<i>Sanicula trifoliata</i> *		epizoochory	Cosmo	genus
<i>Sassafras albidum</i>		endozoochory	Tertiary	genus
<i>Sceptridium dissectum</i>		spore	Tertiary	genus
<i>Scrophularia marilandica</i>		none	Cosmo	genus
<i>Scutellaria ovata</i>		none	Cosmo	genus
<i>Sedum ternatum</i> *		tiny	NTemp	genus
<i>Sicyos angulatus</i>		epizoochory	Tropical	genus
<i>Silene ovata</i> *†		none	NTemp	genus
<i>Silene stellata</i>		none	NTemp	genus
<i>Silene virginica</i>		none	NTemp	genus
<i>Sisyrinchium angustifolium</i>		none	Americas	genus
<i>Smilax bona-nox</i>		endozoochory	Cosmo	subgenus
<i>Smilax glauca</i>		endozoochory	Cosmo	subgenus
<i>Smilax herbacea</i>		endozoochory	Tertiary	subgenus
<i>Smilax hispida</i>		endozoochory	Cosmo	subgenus
<i>Smilax rotundifolia</i>		endozoochory	Cosmo	subgenus
<i>Solidago curtisii</i> †		plume	ENA	subsection
<i>Solidago flaccidifolia</i> †		plume	ENA	subsection
<i>Solidago flexicaulis</i> *		plume	ENA	subsection
<i>Solidago patula</i> *		plume	ENA	subsection
<i>Solidago roanensis</i> †		plume	ENA	subsection
<i>Sorbus americana</i>		endozoochory	NTemp	genus
<i>Sphenopholis nitida</i>		wing	NoAm	genus
<i>Stachys nuttallii</i> *†		none	Cosmo	genus
<i>Stellaria pubera/corei</i> <i>complex</i> *	<i>Stellaria</i> <i>pubera</i>	none	Cosmo	genus
<i>Stenanthium gramineum</i>		none	Tertiary	genus
<i>Symphyotrichum cordifolium</i> *		plume	NoAm	section
<i>Symphyotrichum dumosum</i>		plume	NoAm	section
<i>Symphyotrichum lateriflorum</i>		plume	NoAm	section
<i>Thalictrum clavatum</i> *†		none	Cosmo	genus
<i>Thalictrum coriaceum</i> *†		none	Cosmo	genus

<i>Thalictrum dioicum</i> *		none	Cosmo	genus
<i>Thalictrum hepaticum</i> *†		none	Cosmo	genus
<i>Thalictrum revolutum</i> *		none	Cosmo	genus
<i>Thalictrum thalictroides</i>		none	Cosmo	genus
<i>Thaspium barbinode</i>		wing	ENA	genus
<i>Thaspium trifoliatum</i>		none	ENA	genus
<i>Thelypteris noveboracensis</i>		spore	Tertiary	subgenus
<i>Tiarella cordifolia</i> *		none	Tertiary	genus
<i>Tilia americana</i> *		wing	NTemp	genus
<i>Tipularia discolor</i>		tiny	Tertiary	genus
<i>Toxicodendron radicans</i>		endozoochory	Tertiary	genus
<i>Tradescantia subaspera</i> *		none	Americas	genus
<i>Trillium [catesbaei + grandiflorum]</i> *	<i>Trillium grandiflorum</i>	endozoochory	Tertiary	genus
<i>Trillium [erectum + rugellii + simile + vaseyi]</i> *	<i>Trillium erectum</i>	endozoochory	Tertiary	genus
<i>Trillium luteum</i>		ant	Tertiary	genus
<i>Triphora trianthophora</i>		tiny	Tropical	genus
<i>Tsuga canadensis</i>		wing	Tertiary	genus
<i>Ulmus americana</i>		wing	NTemp	genus
<i>Ulmus rubra</i>		wing	NTemp	genus
<i>Uvularia grandiflora</i> *		ant	ENA	genus
<i>Uvularia perfoliata</i>		ant	ENA	genus
<i>Uvularia sessilifolia</i>		ant	ENA	genus
<i>Vaccinium corymbosum</i>		endozoochory	NTemp	section
<i>Vaccinium erythrocarpum</i> †		endozoochory	Tertiary	section
<i>Vaccinium pallidum</i>		endozoochory	NTemp	section
<i>Vaccinium stamineum</i>		endozoochory	SENA	section
<i>Veratrum parviflorum</i> *†		wing	NTemp	genus
<i>Verbesina alternifolia</i>		wing	Tropical	genus
<i>Verbesina occidentalis</i>		epizoochory	Tropical	genus
<i>Vernonia noveboracensis</i>		plume	Tropical	genus
<i>Viburnum acerifolium</i>		endozoochory	Tertiary	genus
<i>Viburnum lantanoides</i> *		endozoochory	Tertiary	subgeneric clade
<i>Viburnum prunifolium</i>		endozoochory	ENA	subgeneric clade
<i>Vicia caroliniana</i>		none	NTemp	genus
<i>Vinca minor</i>	NA	none	nonnative	NA
<i>Viola [affinis + cucullata + septentrionalis + sororia]</i>	<i>Viola sororia</i>	ant	NTemp	genus
<i>Viola [blanda + incognita + pallens]</i> *	<i>Viola blanda</i>	ant	NTemp	genus
<i>Viola [palmata + subsinuata]</i>	<i>Viola palmata</i>	ant	NTemp	genus
<i>Viola [pennsylvanica + pubescens]</i> *	<i>Viola pubescens</i>	ant	NTemp	genus

<i>Viola canadensis</i> var. <i>canadensis</i> *	<i>Viola</i> <i>canadensis</i>	ant	NTemp	genus
<i>Viola hastata</i>		ant	NTemp	genus
<i>Viola rostrata</i>		ant	NTemp	genus
<i>Viola rotundifolia</i>		ant	NTemp	genus
<i>Viola striata</i>		none	NTemp	genus
<i>Vitis aestivalis</i>		endozoochory	NTemp	subgenus
<i>Xanthorhiza simplicissima</i> *		none	ENA	genus
<i>Zizia trifoliata</i>		none	NoAm	genus

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