BIOGEOGRAPHICAL AND EVOLUTIONARY PROCESSES INFLUENCING THE ASSEMBLY OF DECIDUOUS FOREST PLANT COMMUNITIES

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Ecological theories of community assembly and structuring are often predicated on the overriding importance of small-scale processes operating over short periods of time. However, it is becoming increasingly clear that longer-term, larger-scale processes, such as migration and the diversification of evolutionary lineages, are also important factors influencing the distributions of individual species and the diversity of communities. In this investigation, I first examined the geographic distribution of an ant-dispersed forest plant, *Jeffersonia diphylla*, to assess whether the population structure of its geographic range in eastern North America exhibited patterns consistent with a distribution in equilibrium with the environment, or whether the species' limited dispersal ability on local scales might lead to a non-equilibrial distribution at large geographic scales. Population size and performance did not decline toward the northern range edge and seed sowing within and beyond the species' northeastern range edge demonstrated potentially suitable habitat up to 300 km outside its range. As such, the range of *J. diphylla* may not be in equilibrium with the environment and its restricted distribution in the Northeast may trace to limited post-glacial migration. These findings highlight the potential for limited migratory responses of plant species to climate change, raising the possibility that human intervention or 'assisted colonization' may be necessary to aid some species in tracking modern climate change. Finally, I investigated a prominent plant species richness gradient in the forests of the northeastern U.S. to determine whether long-term evolutionary processes, including phylogenetic niche conservatism, may contribute to high species richness in communities on fertile, calcium-rich soils. Analyses of the phylogenetic 'depth' of communities along this gradient demonstrated that species-rich communities on calcium-rich soils included a disproportionate representation of Basal Angiosperm and Lower Eudicot angiosperm taxa. Parsimony-based reconstructions of the ancestral calcium niche of lineages present in the study also suggested a key role for fertile soils in the early diversification of angiosperms in Temperate Deciduous Forests. These patterns suggest that calcium-rich soils may be an ecological 'zone of origin' for angiosperms and highlight the potential for long-term evolutionary processes to influence species diversity in contemporary communities.

BIOGRAPHICAL SKETCH

Jesse L. Bellemare was born on September 30, 1976 in Northampton, Massachusetts, son of Susan and Robert E. Bellemare, Jr. He attended public schools in Whately and Deerfield, Massachusetts prior to enrolling at the University of Massachusetts in Amherst in 1994. While at the University of Massachusetts, Jesse worked as a research assistant to botanist Dr. Karen Searcy and ecologist Matt Hickler. Jesse graduated in 1998 with a B.S. in Biology and a minor in Portuguese. In 1999, Jesse began research in the Master of Forest Science (MFS) program at Harvard University's Harvard Forest in Petersham, Massachusetts, where he was advised by Dr. David Foster and Glenn Motzkin. For his thesis research, Jesse developed a project investigating environmental and historical factors influencing the distribution of Rich Mesic Forest plant species in western Massachusetts. Following the completion of the MFS degree in 2002, Jesse was accepted to the doctoral program in Ecology and Evolutionary Biology at Cornell University in Ithaca, New York, where he was co-advised by Drs. Monica Geber and Peter Marks. While at Cornell University, Jesse developed research projects focusing on plant migration and community assembly. In July 2006, he married Sarah Ahearn, of Greenfield, Massachusetts. In 2009, Jesse completed his Ph.D. research at Cornell University and began work as a faculty member in the Department of Biological Sciences at Smith College in Northampton, Massachusetts.

to Sarah

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Rock Forest Consortium, Cary Institute of Ecosystem Studies, and the Huyck Preserve; several private landowners also provided access to important study sites. The research described in Chapter 4 was supported in part by a grant from the Kieckhefer Adirondack Fellowship program, administered by the Cornell University College of Agricultural and Life Sciences. Numerous discussions with the Geber, Marks, and Agrawal lab groups at Cornell University provided valuable feedback on the development and interpretation of the research projects described here.

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CHAPTER 1

THE GEOGRAPHIC RANGE OF *JEFFERSONIA DIPHYLLA*, PART I: POPULATION STRUCTURE AND INDIVIDUAL PERFORMANCE IN RANGE CENTER VERSUS RANGE EDGE POPULATIONS

Abstract

Geographic range models predict that species should reach their greatest abundance and highest performance near their range center, with declines in abundance and performance near range edges. While this 'abundant center' range model is premised on species' distributional equilibrium with the environment, dispersal limitation may impede some species' ability to track suitable habitat at a rate that would allow such distribution patterns to develop. I surveyed population-level characteristics and individual-based performance of the ant-dispersed forest herb *Jeffersonia diphylla* in 9 range center and 7 northeastern range edge populations in the eastern United States to test these predictions. No evidence of range edge declines in population size, density, plant size, or reproduction were found. In fact, northeastern range edge populations tended to be larger and denser than range center populations, and individual performance in terms of plant size and reproductive output were significantly higher at the range edge. Correlations between aspects of the abiotic environment, such as soil pH and texture, and plant performance appear to partially explain the existence of highly suitable habitat and vigorous populations at the species' range margin. Further, given that sites with these environmental characteristics occur beyond the current northeastern range edge of *Jeffersonia diphylla*, I infer that the species' distribution may not be in equilibrium with present environmental conditions. Rather, these findings raise the possibility that the range edge of *Jeffersonia diphylla* may represent

a slow-moving, post-glacial colonization front entering the Northeast.

Introduction

Ecological models of geographic ranges often predict that species should achieve their highest abundance and performance near their range center, with declines in abundance and performance toward range edges (Hengeveld & Haeck 1982; Brown 1984; Sagarin & Gaines 2002; Gaston 2003). This pattern has been termed the 'abundant center' distribution model and has even been proposed as a 'general rule' of biogeography (Sagarin et al. 2005). Explanations for this distribution pattern commonly invoke a close correspondence or equilibrium between species ecological niches and their geographic ranges, such that abundance and performance are expected to peak in the range center where environmental conditions are presumed to best match niche requirements (Brown 1984; Sagarin & Gaines 2002). Under these models, range edges are conceived of as the point at which deteriorating conditions along key environmental gradients reduce individual performance and population demographic processes below sustainable levels, driving abundance to zero (Brown 1984; Gaston 2003; Holt et al. 2005; Gaston 2009). Patterns of declining abundance and performance toward range edges have been documented for a number of taxa, particularly bird and insect species (Hengeveld & Haeck 1982; Brown 1984; Gaston 2003). However, the generality of this pattern has also been questioned, with many studies failing to detect the predicted peak in abundance near range centers (Sagarin & Gaines 2002; Gaston 2003; Sagarin et al. 2005; Murphy et al. 2006).

Among the reasons that species may not show a simple abundant-center distribution may be dispersal limitation and migration lags in response to past climate change (Holt et al. 2005; Gaston 2009). In such a scenario, dispersal-limited species may fail to effectively track changing environmental conditions, such that a species' range center may not correspond to the current location of optimal conditions in the environment and some range edges may actually border suitable, but uncolonized, habitat (Skov & Svenning 2004; Holt et al. 2005). The range edges of such species might appear stationary on historical timescales (e.g., decades to centuries), but over longer temporal scales may actually represent slow-moving 'wavefronts' responding to past climate change (Holt et al. 2005). Such a non-equilibrium situation has been hypothesized for the ranges of some plant species (Davis 1986; Skov & Svenning 2004; Van der Veken et al. 2007); however, the possibility of long-term dispersal-limitation of range positions and range edges has only rarely been empirically examined or convincingly documented, and most theoretical models of range edges are premised on species distributional equilibrium with the environment (Holt et al. 2005; Gaston 2009). The potential for species to exhibit substantial time lags in their tracking of climate change has clear implications for species conservation in the face of modern, anthropogenically-driven climate change and should be a high priority for investigation (Skov & Svenning 2004; Van der Veken et al. 2007; Hoegh-Guldberg et al. 2008).

In the Northern Hemisphere glaciation and the extreme climatic changes of the Pleistocene and early Holocene have driven large-scale range dynamics for many plant species (Davis 1983; Huntley & Webb 1989; Williams et al. 2004). In particular, plant species characteristic of Temperate Deciduous Forests grew substantially south of their current distributions in response to climatic cooling in the Pleistocene, and the distributions of many species appear to have been fragmented and marginalized to geographically-restricted refugia (Davis 1983; Bennet et al. 1991; Delcourt 2002). With climatic warming during the Holocene, range expansion from these full glacial refugia has led to the assembly of temperate deciduous forest communities across many formerly-glaciated regions, as well as in areas dominated by boreal-type forest or tundra-steppe vegetation during the Pleistocene (Jackson et al. 2000; Delcourt 2002; Williams et al. 2004).

Paleoecologists and ecologists have vigorously debated the extent to which the post-glacial assembly of plant communities in the north has been limited by seed dispersal and time lags in migration (Davis 1986; Webb 1986; Williams et al. 2001; Van der Veken et al. 2007; Svenning et al. 2008). While patterns in the fossil pollen record have led many paleoecologists to conclude that plant seed dispersal rates have been sufficient to effectively track large-scale shifts in the distribution of suitable habitat (Webb 1986; Clark 1998; Williams et al. 2001), evidence emerging from recent macro-ecological and phylogeographic studies suggests that seed dispersal may have been more limited than originally inferred and that areas of suitable habitat in the north may still be uncolonized (Svenning & Skov 2004; McLachlan et al. 2005; Van der Veken et al. 2007; Svenning & Skov 2007; Svenning et al. 2008).

Among forest plants, those lacking obvious adaptations for long-distance dispersal may be especially likely to exhibit time lags in post-glacial migration and range expansion (Van der Veken et al. 2007). For example, many forest plants produce seeds adapted primarily to local dispersal by ants (myrmecochores), while other species show no obvious morphological adaptations for seed dispersal (barochores; Matlack 1994; Cain et al. 1998). These species often appear to be limited in their ability to colonize new habitat patches and, potentially, to expand their geographic ranges into regions with suitable but unoccupied habitat (Matlack 1994; Bellemare et al. 2002; Verheyen et al. 2003; Van der Veken et al. 2007).

In this study, I investigate the nature of the geographic range of an ant-dispersed forest herb native to eastern North America, *Jeffersonia diphylla* (Berberidaceae). The geographic distribution of *J. diphylla* is centered in the unglaciated central and southeastern United States, but apparently suitable habitat exists beyond the margins of its natural distribution in the formerly-glaciated Northeast. I use surveys of populations at the species' range center and at its northeastern range edge to examine whether population characteristics and individual performance show range edge declines, as would be predicted by abundant-center range models assuming species' distributional equilibrium with the environment, or whether its abundance and performance are comparable or increased near the northern range edge, as might be predicted by non-equilibrium models of dispersal-limited, post-glacial range expansion. Specifically, I investigate whether populations located near the species' range center are larger and denser than range edge populations, and whether population structure shows evidence of more stable populations at the range center than at the range edge. In addition, I examine individual plant performance to determine whether range center plants are larger and more productive than plants growing in populations at the range edge. A second investigation, described elsewhere (Bellemare 2009a), utilizes experimental approaches to test for the existence of suitable habitat beyond the current range edge of *J. diphylla* in the northeastern United States.

Methods

Study Species

Jeffersonia diphylla (Berberidaceae) is a spring-flowering forest herb native to the temperate deciduous forests of eastern North America (Gleason & Cronquist 1991; George 1997). The species is a long-lived perennial that reproduces through both sexual reproduction and asexual, clonal expansion (Smith et al. 1986). Individual plants often include one or more interconnected ramets forming distinct clumps. Each ramet of a clump may include from 2-17 leaves and can produce a single, white flower (Smith et al. 1986). Successful pollination leads to the development of a capsular fruit which, when ripe, opens distally to spill seeds on the ground below the plant (Gleason & Cronquist 1991). The seeds of *J. diphylla* have elaiosomes that encourage dispersal by ants, although the majority of seeds in many populations may be lost to seed predation by rodents (Heithaus 1981; Smith et al. 1986).

The geographic distribution of *J. diphylla* ranges in the south from northwestern Georgia and northeastern Alabama, to central New York, southern Ontario, and southeastern Minnesota in the north (George 1997; Figure 1.1). Throughout its range, *Jeffersonia diphylla* is closely associated with nutrient-rich soils and calcareous bedrock, principally limestone, dolomite, and calcareous shale (Gleason & Cronquist 1991; J. Bellemare, *personal observation*).

Population Characteristics, Structure, and Performance

To evaluate differences in population structure and characteristics between range center and range edge, populations of *J. diphylla* were surveyed in the species' range center in Kentucky, Ohio, and Indiana and at the species' northeastern range edge in western and central New York (Figure 1.1). Population sites were identified via herbarium records and through consultation with local botanists and state Natural Heritage Programs. Nine populations were located in the range center and 7 at the northeastern range edge, for a total of 16 populations (Table 1.1). All *J. diphylla* populations observed had many 100s or 1000s of distinct individuals. Isolated individuals or small populations (e.g., fewer than 100 individuals) are not commonly encountered anywhere in the species' range (J. Bellemare, *personal observation*). All populations located by the author in the two study regions (i.e., range center, range edge) were included in the study, so the survey should represent a relatively unbiased sample of *J. diphylla* population characteristics in these two regions. Surveys were conducted in April-June of 2007 and 2008, with 13 of the 16 populations sampled in both years.

The size, density, percent cover, and life stage structure of *J. diphylla* populations were estimated through sampling of 0.5 x 0.5 m quadrats randomly located along transects through the occupied areas. Within each quadrat, the number of *J. diphylla* individuals was tallied and the species total cover (%) was estimated. Individual plants were classified into three life stages: adults, juveniles, and seedlings. Adult plants were > 20 cm in height, had 4 or more leaves, and were sexually-reproductive (i.e., evidence of flowering) or of comparable size to other sexually-reproductive plants in the population (i.e., in terms of height, leaf size). In many cases, adult individuals were comprised of a clump of two or more interconnected ramets. Plants were counted as distinct individuals if separated by 10 cm or more; while adult *J. diphylla* do expand via clonal spread, field observations and excavations of a limited number of plants suggested that new ramets typically emerge close to established plants (e.g., < 5 cm) and do not extend as far as 10 cm in a single new ramet extension. Juveniles were classified as smaller plants (< 20 cm height) consisting of a single ramet and only 2-3 leaves. Seedlings were identified as small plants (< 10 cm height) having only a single, small leaf. Both juveniles and seedlings may represent plants from more than a single year or cohort, as many plants remain in these life stages for more than one year (J. Bellemare, *personal observation*). Likewise, adult plants may represent individuals that range in age from several years to many decades. Reproductive output of the populations was also assessed in the 0.5 x 0.5 m quadrats. The number of inflorescences was tallied and all ripening fruits in the quadrats were opened to count the number of viable seeds and to assess the number of ovules or seeds that failed to develop. In addition, the number of fruits that had been predated was tallied based on the number of cut or clipped inflorescence stalks present in the plot. To estimate total potential seed output in the absence of

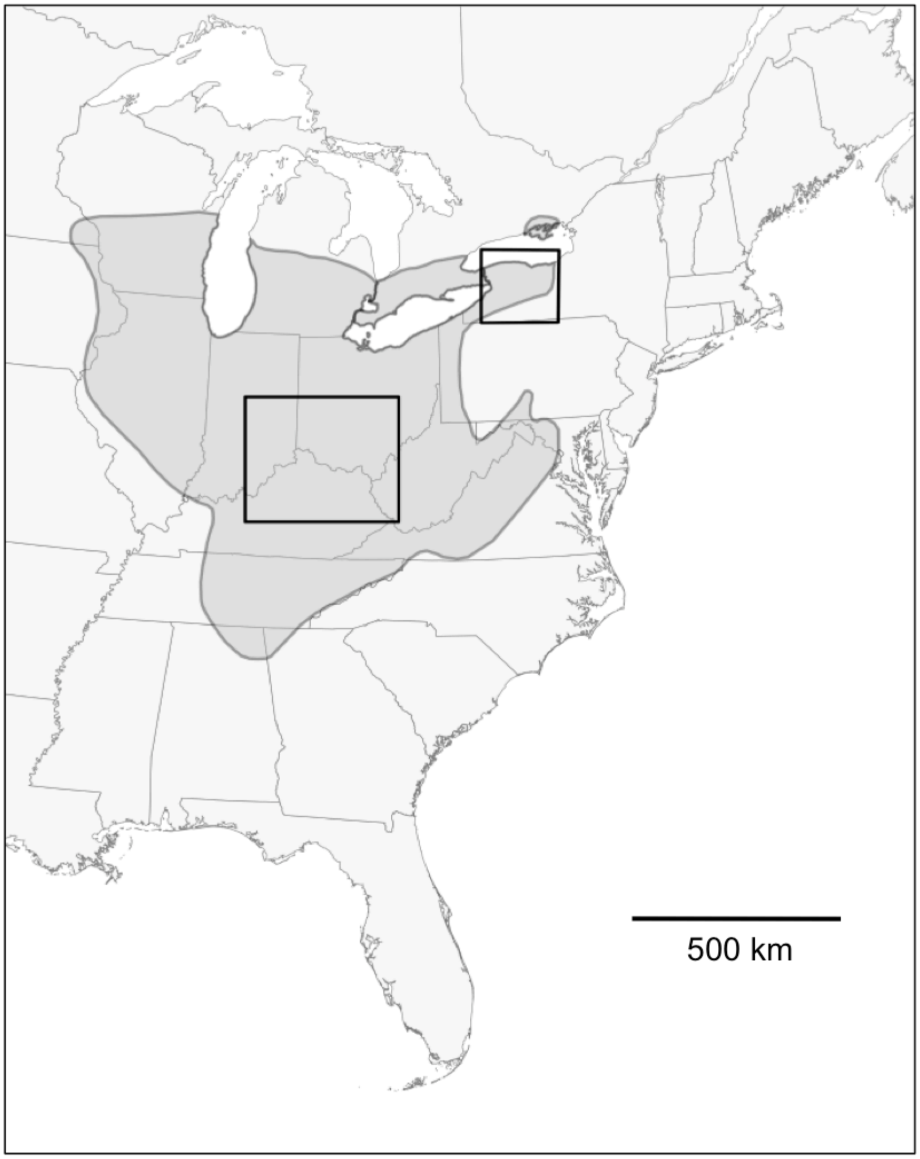

Figure 1.1. The geographic range of *Jeffersonia diphylla* in eastern North America and the two focal regions investigated in this study: the northeastern range edge in central and western New York (small box), and an area near the species' range center in Ohio, Indiana, and Kentucky (large box). The distribution depicted here is based on the range map presented in the *Flora of North America, Vol. 3* and field observations of the author. Two outlying populations in North Carolina and New Jersey are not included on this map.

seed predation, missing fruits were assigned the mean number of seeds contained in the remaining fruits on a given plant, or, if all fruits on the plant had been predated, the missing fruits were assigned the mean number of seeds per fruit observed across the population. The total population size of mature plants was estimated for each population based on average plant density, calculated from the quadrat samples, and the total area (m^2) of the population, estimated by pacing the length and width of the population area.

Differences in population characteristics between range center and northeastern range edge populations of *J. diphylla* were assessed with one-way ANOVA run on population means in JMP 7.0.2 (SAS Institute, Cary, NC). Several variables were natural log-transformed to equalize variances between range center and northeastern range edge samples; in a few cases transformation failed to equalize variances and a Welch's ANOVA, allowing for unequal variances, was used to determine significance. Variables that were natural log-transformed or analyzed with Welch's ANOVA are indicated in Table 1.2. For greater ease of interpretation, results for density-related population characteristics are presented on a per 1.0 m^2 basis, although data were collected in quadrats measuring 0.25 m^2 (i.e., 0.5 x 0.5 m).

Individual Plant Performance

In each of the 16 *J. diphylla* populations surveyed, 11 to 40 sexually-reproductive plants were sampled for performance- and fitness-related traits. The plants included were sexually-reproductive individuals encountered in the randomly-established quadrats (described above), as well as randomly selected sexually-reproductive individuals included to obtain larger sample sizes in low density populations where few reproductive individuals were encountered in plots. The following traits were assessed for each individual: plant height, number of ramets per plant, number of

Table 1.1. Locations of 16 *Jeffersonia diphylla* populations included in this study, their spatial extent, number of random quadrats sampled, and estimated population size of mature plants (to nearest 1000). Sites were sampled between May 2007 and June 2008.

Range Position/ Site Name	**Location**	**Population area (Ha)**	**Quadrats sampled**	**Estimated population size (mature plants)**
Range Center				
Sexton Creek	Clay Co., KY	0.4	44	6,000
Monroe Lake	Monroe Co., IN	0.3	43	6,000
Salt-Peter Cave	Casey Co., KY	0.3	43	5,000
Stroud's Run	Athens Co., OH	0.4	31	5,000
Big Darby	Franklin Co., OH	0.3	20	4,000
Raven Run	Fayette Co., KY	0.2	53	2,000
Fox Lake	Athens Co., OH	0.1	36	2,000
Clifty Falls	Jefferson Co., IN	0.3	35	2,000
Hardy Creek	Trimble Co., KY	0.1	37	1,000
Northeastern Range Edge				
Martisco Woods	Onondaga Co., NY	1.2	43	37,000
Middlesex School	Yates Co., NY	0.8	16	32,000
Keshequa Creek	Livingston Co., NY	0.3	40	7,000
Two Mile Creek	Livingston Co., NY	0.3	43	6,000
Venice Woods	Cayuga Co., NY	0.3	41	6,000
Great Gully	Cayuga Co., NY	0.1	38	1,000
Railroad Mills	Ontario Co., NY	0.2	40	1,000

leaves, length of the 3 largest leaves, number of inflorescences, number of fruits successfully developed, number of fully-developed seeds produced per fruit, number of undeveloped ovules or seeds per fruit, and the total number of fully-developed seeds matured per plant. Data on a subset of these traits was collected in 2007, while all traits were assessed in 2008; sample sizes for each trait are provided in Table 1.3.

Each region was sampled to allow observation of seed maturation immediately prior to fruit dehiscence (i.e., mid- to late-May in the range center, mid- to late-June at the northeastern range edge). In all populations, the developing fruits were estimated to be within 1-2 weeks of dehiscing, with nearly-mature or fully-mature seeds inside. Undeveloped ovules and aborted seeds were readily differentiated from fully-developed seeds by substantial differences in size, shape, and coloration (i.e., < 50% size of viable seeds, often wrinkled rather than smooth, and pale in color relative to viable seeds). Surveys were conducted in 2007 and 2008 for range center populations, with 8 of 9 the populations surveyed in each year; at the northeastern range edge, 7 populations were surveyed in 2007, with 6 of these sites revisited in 2008. Differences in individual plant performance between range center and northeastern range edge populations were assessed with one-way ANOVA run on mean values for each population in JMP 7.0.2.

Abiotic and Biotic Environment

To quantify basic features of the abiotic environment of each population, site slope and aspect were measured, and 3-4 soil cores were collected for chemical and physical analyses of soil characteristics. Soil cores were collected using a polyvinyl chloride (PVC) corer with an inside diameter of 5.3 cm; cores extended from 0 to 10 cm depth in the mineral soil for a total volume of ~ 220 cm^3. Leaf litter and surface organic (O) layer material were excluded from the soil samples. Soil bulk density (g/cm^3) was calculated for each sample based on its dry weight after being oven-dried for 48 hours at 50° C; pebbles and rocks > 2 mm sieved from the soil samples were excluded from bulk density calculations. Following estimation of bulk density, soil samples from within each site were combined and thoroughly mixed. Subsamples of these pooled samples were submitted to Brookside Laboratories, Inc. (New Knoxville, OH) for analysis of physical and chemical characteristics, including soil texture, organic matter content, pH, and cation concentrations.

In addition to edaphic and physiographic features of individual population sites, basic climatological data were compiled for the two study regions from the National Climate Data Center CLIMOD database (http://www.ncdc.noaa.gov). For each population site, data on monthly mean temperatures and precipitation at the nearest weather station for the period 1971-2000 were accessed. Weather stations were in the same county for 14 of the 16 population sites, and within 50 km distance for all sites. Analyses of precipitation focused on the primary growing season for *J. diphylla*: March through June in the range center and April through July at the northeastern range edge (Baskin & Baskin 1989; J. Bellemare, *personal observation*). This is the period of time when seeds germinate and established plants emerge, produce leaves, and reproduce; plants often senesce for the year in mid- to late-summer (Baskin & Baskin 1989; J. Bellemare, *personal observation*).

Several aspects of the biotic environment of *J. diphylla* populations were also assessed, these included: species richness of plant species other than *J. diphylla* in the sampled quadrats, total herbaceous layer cover and cover of species other than *J. diphylla*, importance of *J. diphylla* relative to the cover of other plant species, and rates of seed predation by rodents. Herbivory on *J. diphylla* leaves, by invertebrate or vertebrate herbivores, was rarely observed in either study region, even in areas with clear signs of white-tailed deer (*Odocoileus virginainus*) impacts on other forest plant species (J. Bellemare, *personal observation*). The individual-level impacts of seed predation were estimated by comparing the expected number of seeds that might have been produced by a plant had all destroyed fruits been allowed to mature; destroyed fruits were assigned the mean number of seeds produced per remaining, intact fruit on a given plant; if all fruits on a plant were destroyed, the destroyed fruits were assigned the mean number of seeds produced per fruit based on calculations across the whole population. Importantly, these estimates of seed predation assume that seed predators consume all seeds in destroyed fruits; however, it is possible that some seeds cached by seed predators may never be retrieved, leading to seed dispersal rather than seed predation.

Differences in the abiotic and biotic environment between range center and range edge were tested with one-way ANOVA run on mean values for each population site. Several soil-related factors (e.g., organic matter content, silt and clay content) were natural log-transformed to equalize variances and improve normality. Prior to analysis, site aspect was converted to a Heat Load Index value ranging from 0 to 1, following McCune and Grace (2002), because aspect is not well-suited to direct analysis (e.g., aspects of 1° and 360° are almost equivalent). Specifically, sites with a southwest aspect that are expected to receive the greatest heat load were assigned the highest index value (1) and sites with a northeast aspect that are expected to receive the lowest heat load were assigned the lowest index value (0); index values are symmetrical around this northeast to southwest axis. Mean annual and monthly temperature data for the range center and northeastern range edge exhibited unequal variances, even after transformation; consequently, these data were analyzed using Welch's ANOVA. In terms of the biotic environment, results for species richness are presented on a per 0.25 m^2 basis. Conversion of species richness data to 1.0 m^2 basis, as was done for density-related characteristics of *J. diphylla* populations, was not feasible, as species accumulation per unit area is typically not linear, making simple extrapolation problematic (McCune & Grace 2002).

In order to assess relationships between continuous environmental variables and aspects of *J. diphylla* population structure and individual performance, Pearson product moment correlations ("Pearson's r") were calculated between a subset of environmental factors and population characteristics (e.g., cover %, density, seed production per m^2) and performance of sexually reproductive individuals (e.g., plant height, ramet number, inflorescence number, seed production). These correlation analyses were only run for pairs of factors exhibiting distributions meeting assumptions of normality (e.g., based on Shapiro-Wilk Goodness-of-Fit test). Pearson correlations were calculated in JMP 7.0.2. It was not possible to analyze correlations between all pairs of continuous variables, as a number of factors exhibited non-normal, bi-modal distributions corresponding to significant differences between range edge and range center observations.

Results

General Population and Site Characteristics

Across the 16 populations surveyed, a total of 603 quadrats were sampled, with 16 to 53 quadrats sampled per population (mean: 38 quadrats ± 2.3 SE per site). Populations of *J. diphylla* were relatively large and dense when compared to other forest herbs, with a mean density of 1.8 (± 0.2 SE) adult plants per m^2 and all populations estimated to number in the 1000s or 10,000s of individuals (Table 1.1). In both regions, populations of *J. diphylla* occupied distinct areas in the landscape surrounded by large expanses of unoccupied habitat; the mean area occupied by populations was 0.3 ha (± 0.07 SE), with a range from 0.06 to 1.2 ha. Within occupied areas, the relative importance of *J. diphylla* compared to other plant species was high:

J. diphylla comprised approximately 20% (± 2.9 SE) of total herb layer cover on average, with some populations comprising as much as 41% of total herb layer cover; in the latter cases, *J. diphylla* was the most abundant herb layer plant species present. In terms of life stage structure, populations were comprised of ~ 50% adult individuals on average, with ~ 15% juveniles and ~ 35% seedlings.

Population Characteristics, Structure, and Performance

Populations of *J. diphylla* in the range center and at the northeastern range edge were comparable in life stage structure, but showed trends toward differences in density and total size, and exhibited highly significant differences in cover. In terms of population size, the mean number of adult plants per population at the northeastern range edge (12,900 ± 5719 SE) was greater than estimates for populations at the range center (3978 ± 691 SE), although this difference was not significant (Table 1.2). The greater average size of northeastern range edge populations was due to the presence of two very large populations in this region (estimated to contain over 30,000 mature plants each); the remaining 5 populations at the range edge overlapped in size with range center populations (mean 4216 vs. 3978 mature plants, respectively).

Populations of *J. diphylla* at the northeastern range edge exhibited a trend toward higher density of adult plants (2.4 plants/m^2) than range center populations (1.4 plants/m^2), although this pattern was only marginally significant ($p = 0.10$; Table 1.2). Similarly, mean densities of juveniles and seedlings tended to be somewhat higher in northeastern range edge populations (mean: 0.7 juveniles/m^2; 1.5 seedlings/m^2) than in range center populations (mean: 0.4 juveniles/m^2; 1.4 seedlings/m^2), although these trends were not significant (Table 1.2).

In contrast to population size and density, northeastern range edge populations exhibited cover values almost 4 times higher than populations near the range center (mean cover 17.1% vs. 4.5%, respectively; $p < 0.001$; Table 1.2). This translated to significantly greater relative importance of *J. diphylla* at the northeastern range edge (28.5 % of total herb layer cover) than in the range center (13.7% of total herb layer cover; $p < 0.01$).

Population structure was remarkably similar between the northeastern range edge and range center of *J. diphylla*. On average, populations at the range edge included 52% adult plants, 14% juveniles, and 34% seedlings, while populations at the range center included 48% adult plants, 15% juveniles, and 37% seedlings. Tests of differences in population structure between northeastern range edge and range center populations were entirely non-significant ($p > 0.75$) in all 3 cases (i.e., adult, juvenile, seedling; Table 1.2).

Substantial differences occurred in population-level estimates of sexual reproduction between range center and northeastern range edge populations. In particular, northeastern range edge populations produced ~ 10 times more inflorescences per unit area than range center populations (7.3 vs. 0.7 inflorescences/m^2, $p < 0.0001$; Table 1.2). On average, actual reproductive output of populations at the northeastern range edge was ~ 4 times higher per unit area than range center populations (56.7 vs. 14.6 seeds per m^2, respectively); however, this difference was only marginally significant ($p = 0.0671$), due in large part to significantly higher rates of seed predation by rodents at the northeastern range edge (~56% of fruits predated) when compared to range center populations (~15% of fruits predated; Table 1.2). Interestingly, in both regions, fruit predation varied substantially between populations (e.g., ranging from ~5 to 97% of fruits predated in range edge populations, and from ~0 to 50% of fruits predated in range center populations; data not shown). In the absence of seed predation, the estimated potential reproductive output of northeastern range edge populations was ~ 10 times higher than that estimated for range center populations (167.0 vs. 16.7 seeds per m^2, $p < 0.001$; Table 1.2).

Individual Plant Performance

In total, 499 sexually reproductive plants were examined for performance-related traits, including 264 plants in range center populations and 235 plants in northeastern range edge populations. Some traits, such as plant height, number of inflorescences, and seed production, were measured on all plants in 2007 and 2008, while other traits, such as number of ramets and leaf size, were measured only in 2008 (sample sizes for each trait are provided in Table 1.3).

In general, *J. diphylla* plants growing in populations at the northeastern range edge were substantially larger than plants growing in populations at the range center. Specifically, the mean height of range edge plants was ~ 31% greater than range center plants (37.1 vs. 28.4 cm; $p < 0.0001$). Further, range edge plants included more ramets than range center plants (7.4 vs. 1.8 ramets per plant; $p < 0.0001$) and more leaves per plant (38.1 vs. 9.0 leaves; $p < 0.0001$; Table 1.3). In addition, the mean length of the three largest leaves on plants was significantly greater at the northeastern range edge than at the range center (13.7 vs. 11.9 cm; $p < 0.001$). In a subsample of 170 leaves, leaf length was found to be highly correlated ($R^2 = 0.96$; $p < 0.0001$) with total leaf area (cm^2), indicating that the greater length of leaves produced by plants at the range edge also likely results in substantially greater surface area per leaf.

In regards to sexual reproduction, plants at the northeastern range edge produced significantly more inflorescences than individuals at the range center (5.2 vs. 1.2 inflorescences per plant; $p < 0.0001$, Table 1.3). Since only one inflorescence is produced per ramet (Smith et al. 1986), this pattern presumably from the greater

Table 1.2. Characteristics, structure, and performance of *Jeffersonia diphylla* populations near the species' range center and at the species' northeastern range edge in the eastern United States. Values presented are means ± standard error; p-values are for F-ratio of one-way ANOVA run on population means. Significant p-values are highlighted in bold font. The following variables were natural log transformed prior to analysis to equalize variances and improve normality: inflorescences/m^2, % fruits failed, % fruits predated, observed seed production, and potential seed production. Sample sizes: range center = 9 populations, 342 plots; northeastern range edge = 7 populations, 261 plots.

Population Characteristic	**Range Center**	**Northeastern Range Edge**	**p-value**
Population size: mature plants	3798 ± 691	12921 ± 5719	0.1629
Density: mature plants/m^2	1.4 ± 0.2	2.4 ± 0.4	0.1018
Density: juveniles/m^2	0.4 ± 0.1	0.7 ± 0.2	0.1930
Density: seedlings/m^2	1.4 ± 0.4	1.5 ± 0.5	0.7442
Cover (%)	4.5 ± 0.6	17.1 ± 3.4	**0.0004**
Importance (relative % cover)	13.7 ± 3.0	28.5 ± 3.4	**0.0039**
Population structure: mature plants %	48.4 ± 5.4	51.5 ± 8.4	0.7507
Population structure: juveniles %	14.8 ± 2.1	14.4 ± 2.5	0.9132
Population structure: seedlings %	36.8 ± 6.1	34.1 ± 10.3	0.8126
Inflorescences/m^2	0.70 ± 0.20	7.28 ± 1.56	**< 0.0001**
Fruits failed (%)†	14.8 ± 10.5	0.5 ± 0.3	0.1341
Fruits predated (%)	11.8 ± 7.3	55.8 ± 14.3	**0.0059**
Fruits successfully matured (%)	73.4 ± 11.9	43.7 ± 14.4	0.1320
Observed reproductive output (# seeds/m^2)	14.6 ± 14.6	56.7 ± 16.5	0.0671
Potential reproductive output, no predation (# expected seeds/m^2)	16.7 ± 26.0	167.0 ± 29.5	**0.0002**

†Data analyzed with Welch's ANOVA, allowing for unequal variance among groups.

number of ramets produced by plants at the northeastern range edge (Table 1.3). These differences carried through to seed production per plant, with range edge plants producing, on average, ~ 2 times more seed than range center plants (58.2 vs. 28.4 seeds per plant, $p = 0.0380$). However, the magnitude of this difference was partially obscured by high seed predation in some northeastern range edge populations: potential seed production per plant, in the absence of seed predation, was almost 4 times higher in northeastern range edge populations than range center populations (121 seeds vs. 31 seeds per plant, respectively; $p < 0.0001$, Table 1.3). Notably, seed production per successfully-matured fruit was comparable between northeastern range edge and range center plants (21.9 vs. 24.1 seeds per fruit, respectively; $p > 0.10$) and the rate at which ovules and seeds failed to develop within these fruits was also similar (16.6% vs. 17.5% failed; $p > 0.10$; Table 1.3). Thus, the significant differences in reproductive output trace almost entirely to the greater number of inflorescences produced by northeastern range edge plants compared to range center plants.

Range Center vs. Range Edge: Abiotic and Biotic Environment

All the sites occupied by *J. diphylla* populations exhibited slightly acidic to circumneutral soils (mean pH 6.0, range 5.1 to 7.4). The relatively high pH of the soils was apparently driven by high concentrations of calcium cations in the soil (mean = 2913 parts per million ± 209 SE; Table 1.4), with calcium cations representing between 43-85% of total cations (mean = 69%, data not shown). The calcium enriching the soils at these sites is likely derived from the weathering of calcareous limestone bedrock underlying the sites or exposed in ledges and bedrock outcrops nearby (J. Bellemare, *personal observation*).

In terms of physiography, the abiotic environment of *J. diphylla* populations in the range center and at the northeastern range edge was relatively similar (Table 1.4).

The slope and aspect of population sites did not differ significantly between the range center and northeastern range edge; further, the Heat Load Index of sites, based on site aspect, was comparable (Table 1.4). In terms of edaphic conditions, calcium content and organic matter did not differ significantly between range center and range edge sites; however, soil texture did differ significantly: soils at northeastern range edge sites had significantly greater sand content and tended to have lower clay content than range center sites (38.4 vs. 26.9% sand, $p = 0.04$; 12.2 vs. 17.1% clay, $p = 0.09$; Table 1.4). In addition, there was a marginally significant trend toward higher soil pH at range edge sites than at range center sites (pH 6.2 vs. 6.7, $p = 0.08$; Table 1.4). Mean monthly temperatures recorded at weather stations located near the study sites differed significantly between the range center and northeastern range edge ($p < 0.0001$), with range center sites being significantly warmer in all months (data not shown). For example, mean temperature during the coldest month (January) was ~ 4°C warmer in the range center than at the northeastern range edge (-0.7° vs. -4.8°C), and temperature during the warmest month (July) was ~ 2.4°C higher in the range center (23.9° vs. 21.5°C; Table 1.4). Mean precipitation during the primary growing season of *J. diphylla* was significantly higher in the range center than at the northeastern range edge (42.4 cm precipitation for March-June in range center, 32.7 cm for April-July at range edge; $p = 0.0003$; Table 1.4).

Pearson correlations testing relationships between a subset of abiotic factors and population-level characteristics detected a significant positive correlation between soil sand content and *J. diphylla* frequency, cover, and density of mature plants. This pattern was mirrored by negative correlations between these population-level characteristics and the silt and clay content of soils (Table 1.4). Significant negative correlations were also detected between site slope and the density of seedlings and total density of populations (Table 1.4). Pearson correlations between the abiotic

Table 1.3. Individual-based performance metrics of *Jeffersonia diphylla* in range center and northeastern range edge populations. Values are means ± standard error; p-values are based on F-ratio of one-way ANOVA run on population means. Significant p values are highlighted in bold font. The following variables were natural log-transformed prior to analysis to equalize variances and improve normality: ramets per plant, leaves per plant, inflorescences per plant, potential seeds per plant, and percent ovules and seeds undeveloped. Sample sizes for each trait are provided in column 5, following the form: range center populations N (individuals n), range edge populations N (individuals n).

Plant Trait	Range Center	Northeastern Range Edge	p-value	Sample sizes
Plant height (cm)	28.4 ± 0.7	37.1 ± 0.8	**< 0.0001**	9 (262); 7 (234)
Ramets per plant	1.8 ± 0.4	7.4 ± 0.5	**< 0.0001**	8 (177); 6 (125)
Leaves per plant	9.0 ± 3.1	38.1 ± 2.9	**< 0.0001**	6 (109); 7 (155)
Largest leaf length (cm)†	11.9 ± 0.3	13.7 ± 0.3	**0.0007**	9 (198); 7 (140)
Inflorescences per plant	1.2 ± 0.4	5.2 ± 0.4	**< 0.0001**	9 (264); 7 (235)
Seeds per plant†	28.4 ± 8.1	58.2 ± 9.2	**0.0380**	9 (254); 7 (218)
Potential seeds per plant, without predation	30.8 ± 10.8	121.2 ± 12.3	**< 0.0001**	9 (254); 7 (235)
Seeds per fruit	24.1 ± 1.3	21.9 ± 1.5	0.2748	9 (254); 7 (218)
Percent (%) ovules and seeds undeveloped	17.5 ± 2.4	16.6 ± 2.7	0.9493	9 (254); 7 (218)

†Data were analyzed with Welch's ANOVA, allowing for unequal variances among groups.

environment and performance of *J. diphylla* individuals were run for a subset of traits, including plant height, seeds per fruit, percent undeveloped seeds and ovules, and expected seeds per plant in the absence of seed predation. Of these, a significant positive correlation was detected between plant height (cm) and soil pH ($r = 0.64$, $p < 0.01$; Table 1.4); other correlations were non-significant. The relationship between abiotic factors and the individual performance traits ramets per plant, inflorescences per plant, leaves per plant, and mean largest leaf were not analyzed, as data for these traits were strongly bimodal (i.e., non-normal) due to significant overall differences between range center and range edge populations (Table 1.3). Likewise, Pearson correlations were not conducted for climatic variables due to significant differences in temperature and precipitation between the range center and range edge regions (i.e., data were bimodally distributed; Table 1.4).

The biotic environment differed substantially between range center and northeastern range edge population sites. In terms of the competitive environment experienced by *J. diphylla*, species richness (excluding *J. diphylla*) in plots was significantly lower at range edge sites than at range center sites (2.9 spp/0.25 m^2 vs. 4.3 spp/0.25 m^2, respectively; $p = 0.0239$); however, herbaceous layer cover (excluding *J. diphylla*) was comparable between range center and range edge sites (27.3 vs. 22.8%, $p = 0.5027$; Table 1.4). More importantly from a reproductive standpoint, fruit predation rates at the northeastern range edge were significantly higher than range center populations (covered previously). Nevertheless, despite these high fruit predation rates, mean seed production per m^2 in range edge populations still exceeded range center populations due to the significantly greater number of inflorescences initiated per plant (Tables 1.2, 1.3). No significant correlations were detected between features of the competitive environment (i.e., species richness and cover of plant species other than *J. diphylla*) and aspects of population or individual

Table 1.4. Environmental characteristics of *Jeffersonia diphylla* population sites and their relation to population and plant performance at the species range center and northeastern range edge. Values presented for each region are population means ± SE; p-values are based on F-ratio of one-way ANOVA run on population means. Only performance metrics exhibiting a significant Pearson's correlation with the abiotic or biotic factor are listed in column 5. The following variables were natural log transformed prior to analysis to equalize variances and improve normality: soil silt, clay, and organic matter content.

	Range Center	**Northeastern Range Edge**	**p value**	**Significant Pearson's correlations (r)**
Abiotic factors:				
Soil pH	6.2 ± 0.2	6.7 ± 0.2	0.0822	Plant height (r = 0.64**)
Soil calcium p.p.m.†	2816 ± 286	3038 ± 324	0.5780	No significant correlations
Soil sand content (%)	26.9 ± 3.3	38.4 ± 3.7	**0.0365**	*J. diphylla* frequency% (r = 0.52*); cover % (r = 0.67**); density mature plants/m^2 (r = 0.70**); potential seeds/m^2 (r = 0.50*)
Soil silt content (%)	56.1 ± 3.2	49.4 ± 3.7	0.1962	Density mature plants/m^2 (r = -0.54*)
Soil clay content (%)†	17.1 ± 1.9	12.2 ± 2.1	0.0881	*J. diphylla* cover % (r = -0.62*)
Soil organic matter (%)†	7.5 ± 0.7	6.9 ± 0.8	0.5279	No significant correlations
Site Slope (°)†	23.0 ± 2.4	17.9 ± 2.7	0.2173	Density seedlings/m^2 (r = -0.51*); total density/m^2 (r = -0.67**);
Soil bulk density (g/cm^3)	0.80 ± 0.06	0.95 ± 0.07	0.1260	No significant correlations
Site Aspect (°)	136 ± 29	141 ± 33	NA	Not tested, factor unsuitable for direct analysis

Table 1.4 (continued)

Heat Load Index	0.50 ± 0.10	0.35 ± 0.11	0.3227	No significant correlations
Mean annual temperature (°C)†	12.2 ± 0.3	8.6 ± 0.1	**<0.0001**	Not tested, bimodal distribution
January mean temperature (°C)†	-0.7 ± 0.5	-4.8 ± 0.1	**< 0.0001**	Not tested, bimodal distribution
July mean temperature (°C) †	23.9 ± 0.3	21.5 ± 0.1	**< 0.0001**	Not tested, bimodal distribution
Growing season mean precipitation (cm)	42.4 ± 1.7	32.7 ± 1.1	**0.0003**	Not tested, bimodal distribution
Biotic factors:				
Species richness per 0.25 m^2, excluding *Jeffersonia diphylla*	4.3 ± 0.3	2.9 ± 0.4	**0.0239**	No significant correlations
Herb layer cover %, excluding *Jeffersonia diphylla*	27.3 ± 4.4	22.8 ± 5.0	0.5027	No significant correlations
Seed predation (% fruits missing)	11.8 ± 7.3	55.8 ± 14.3	**0.0230**	Not tested

† = Data were analyzed with Welch's ANOVA, allowing for unequal variances among groups.

* = Pearson's correlation p value < 0.05; ** = Pearson's correlation p value < 0.01.

performance (e.g., *J. diphylla* density, expected seed production/m^2).

Discussion

The results of this study demonstrate that patterns of abundance and performance for *J. diphylla* do not follow predictions derived from simple abundant-center range models; rather, populations at the species' northeastern range edge were some of the largest and densest observed, and plants in these populations were substantially larger and more productive than range center individuals. In fact, the largest population documented in the study ('Martisco Woods'), estimated to include well over 30,000 adult plants, occurred near the species' range edge in the Northeast (Table 1.1). Similarly, the largest and most productive individual plant documented anywhere in the geographic range of *J. diphylla* also occurred in this range edge population in central New York. These findings appear consistent with non-equilibrium range models hypothesizing long-term time lags in the post-glacial range expansion of dispersal-limited plant species into suitable, but uncolonized, areas of potential habitat in the north (Van der Veken et al. 2007; Svenning et al. 2008).

Population Characteristics and Individual Performance

Contrary to predictions of the abundant-center model (Sagarin & Gaines 2002; Gaston 2003), the results of this study show no evidence of declining abundance or performance in range edge populations of *J. diphylla* relative to range center populations. These results agree with those of a number of other plant studies. For example, in a study comparing range center and range edge populations of *Aquilegia canadensis* in eastern North America, Herlihy and Eckert (2005) found no evidence of declines in population size, density, or performance at the species' northern range margin. Similarly, Samis and Eckert (2007) found little evidence to support the abundant-center range model for two coastal dune plant species. More broadly, a recent macro-ecological analysis of tree species distributions and abundances in eastern North America concluded that the majority of the 134 tree species reviewed did not exhibit a clear abundant-center distribution (Murphy et al. 2006). Overall, these results and those of similar studies have cast considerable doubt on the prevalence of abundant-center distributions (Sagarin & Gaines 2002; Gaston 2003).

Despite limited evidence for simple abundant-center distributions in many plant species, a number of studies focused more specifically on plant range edges have documented declines or failures in reproduction and recruitment at or beyond range margins, often linked to climatic factors (Kavanagh & Kellman 1986; Woodward 1987; Carey et al. 1995; Gaston 2003; Gaston 2009). However, in the present study, there was no clear evidence for such demographic declines: the life stage structures of populations in the range center and at the range edge were remarkably similar (Table 1.2). This finding suggests that no major differences in population dynamics or viability exist between range center and northeastern range edge populations of *J. diphylla* (Hegland et al. 2001), as would be expected if environmental conditions at the range edge were sub-optimal or more variable relative to range center conditions (Brown 1984; Kavanagh & Kellman 1986; Nantel & Gagnon 1999; Holt et al. 2005; Gaston 2009). In general, the population structure documented for both range center and range edge sites suggests relatively stable populations, characterized by long-lived adult plants and limited recruitment due to low survival of seedlings and juveniles. Population dynamics of this nature appear to be characteristic of a number of perennial forest herbs adapted to the relatively stable conditions of closed-forest habitats (Bierzychudek 1982; Whigham 2004).

The Abiotic Environment

Although the physiographic settings of range center and range edge populations were similar in terms of slope and aspect, significant differences were detected in a subset of the abiotic and biotic factors examined. For example, soil texture differed substantially between the two regions, with soils at range edge sites having significantly higher sand content than range center sites (38% vs. 27%, respectively; Table 1.4). Such environmental differences may explain some of the variation observed in population- and individual-level performance between range center and range edge populations of *J. diphylla*. Results of Pearson correlation analyses indicated that *J. diphylla* populations growing on sites with greater soil sand content had higher density, cover, and potential seed output than populations on finer textured soils with lower sand content (Table 1.4). These positive correlations between sand content and aspects of population performance were apparent even *within* regions (although not always significant), indicating that the effect of this abiotic factor was not due to its simply being confounded with other regional differences (e.g., unmeasured climatic variables); rather, soil texture may potentially explain some of the differences in *J. diphylla* population structure and performance documented between the two regions.

There are several mechanisms by which soil texture might influence the density and performance of *J. diphylla* populations. Most prominently, soil sand content affects water availability, drainage, and aeration (Brady 1990). The lower sand content and higher clay content of range center population sites may lead to decreased soil aeration during wet conditions (Brady 1990), and given the substantially higher precipitation levels in the range center (~ 30% more rain) during the primary growing season, this effect might be exacerbated. Further, poor aeration of clay-rich soils under wet conditions may also lead to decreases in N mineralization and nitrification rates, lowering N availability to plants (Brady 1990; Zak & Grigal 1991; Grigal & Homann 1994). At the opposite extreme, clay-rich soils may also be prone to increased droughtiness during excessively dry conditions due to the greater strength with which soil water is held in the small pores of clay-rich soils (Brady 1990; Whitmore 2000). Taken together, these characteristics of finer-textured, clay-rich soils found in the range center could potentially reduce the survival and growth of individual *J. diphylla* plants, as well as impacting overall population density, cover, and seed output.

The significant differences detected in soil texture between range center and range edge population sites come in spite of similar underlying bedrock geology. Both regions lie in the Central Lowland Physiographic Province of eastern North America, an area underlain primarily by fine-textured sedimentary bedrocks of Paleozoic marine origin, including shale, siltstone, claystone, limestone, and dolomite (Fenneman 1938; Rickard & Fisher 1970; Roberts 1996; Slucher et al. 2006). Soils derived from the weathering of shale, siltstone, and claystone tend to be fine-textured and clay-rich, reflecting the composition of the parent bedrock (Bailey 2000); the weathering products of pure limestone or dolomite are water soluble and thus do not form soil, but these bedrock types often contain soil-forming impurities and are frequently interlayered with fine-textured shales that do produce soil when weathered (Brady 1990; Samonil 2007). Near the range center, soils are primarily developed in residuum and colluvium derived from the *in situ* weathering of the local sedimentary bedrock. In contrast, the northeastern range margin of *J. diphylla* lies entirely within areas glaciated during the Pleistocene and soils in this region have developed in a variety of glacial deposits, including glacial till, outwash, or the lacustrine deposits of late Pleistocene peri-glacial lakes (Flint 1971; Muller 1977; Cadwell et al. 1986; Bailey et al. 2004). As such, the higher sand content of soils over otherwise fine-textured bedrock likely reflects the allochthonous origin of the parent material (e.g., glacial till or outwash), potentially including coarse-textured sediments derived from areas to the north via glacial transport (e.g., crystalline rocks of the Canadian Shield begin ~ 200 km north of *J. diphylla* population sites in New York). In parallel, till and outwash deposits may also be coarser textured due to the removal of fine-textured sediments by water during collapse and melting of the ice sheet (Flint 1971). Notably, even if these till-derived soils were not highly calcareous when initially deposited, the relatively rapid weathering of underlying limestone or calcareous shale would likely produce local calcium enrichment and increased soil pH (Hornbeck et al. 1997; Press et al. 2003; Bailey et al. 2004).

In addition to soil texture, soil pH also exhibited a significant correlation with *J. diphylla* performance, in particular, plant height (Table 1.4). Specifically, plants growing on higher pH, circum-neutral soils (e.g., pH 6-7.5) were taller than plants growing on lower pH, weakly acidic soils (e.g., pH 5-6). Nonetheless, all population sites exhibited soils with relatively high pH when compared to the more acidic upland forest soils typical of most of the eastern United States (e.g., pH 4-5; Vitousek 1984; Boettcher & Kalisz 1990; Peet et al. 2003; Bellemare et al. 2005; McCarthy & Brown 2006; Fabio et al. 2009). The observed association of *J. diphylla* with high pH soils is consistent with earlier, qualitative statements on the high pH edaphic niche of the species (e.g., Gleason & Cronquist 1991). The positive correlation between soil pH and plant height was also significant for range center sites when considered alone (Pearson correlation $r = 0.78$, $p < 0.05$), suggesting that the correlation between soil pH and height was not confounded by other, unmeasured environmental differences between the range center and range edge. Nevertheless, mean soil pH tended to be higher at northeastern range edge sites than at range center sites, although this difference was only marginally significant ($p = 0.08$; Table 1.4). This regional trend in soil pH may partially account for the significantly greater height of range edge plants when compared to range center plants (Table 1.3).

The correlation between plant height and soil pH may derive from the numerous effects pH has on soil chemistry and nutrient availability to plants (Brady 1990; Lee 1999). Increased soil pH may lead to higher rates of nitrification and plant available N (Goodale & Aber 2001; Christopher et al. 2006), while, conversely, increased H^+ concentration in lower pH soils may interfere with root growth and nutrient uptake (Brady 1990; Lee 1999). The comparatively high pH of sites occupied by *J. diphylla* likely traces to the presence of limestone or other carbonate-rich bedrock close to or at the soil surface (J. Bellemare, *pers. obs.*). As these bedrocks weather, they release Ca^{2+} cations into the soil solution, displacing H^+ from the soil and increasing soil pH (Brady 1990). Beyond its direct effects on soil chemistry, calcium is also an important plant nutrient with several key functions in cellular physiology (McLaughlin & Wimmer 1999). As such, calcareous high pH soils may allow for the growth of larger and more vigorous plants.

Overall, the soil-related results indicate that highly suitable habitat for *J. diphylla* exists near its northeastern range margin and, in fact, that the glacial history of this region probably contributed to the development of coarser-textured, calcareous soils that appear to be ideal for the species. Interestingly, evidence from geologic maps, soil sampling, and the distribution of other plant species specialized on calcareous soils (‘calciphiles’) suggests that potentially suitable, but uncolonized, habitat for *J. diphylla* may exist even further to the north and east of its current range margin (Bellemare et al. 2005); this possibility will be explored in more detail in a subsequent paper (Bellemare 2009a). More broadly, these findings highlight the key role that geologic and edaphic factors may play in driving the distribution and abundance of plant species with strong edaphic preferences (e.g., calciphiles, serpentine specialists). Further, because the spatial patterning of geologic and edaphic conditions in the environment is often highly complex, this raises the possibility that the distributions and abundances of plant species with specialized edaphic niches may be particularly unlikely to exhibit simple abundant-center distributions.

Finally, while abiotic factors related to climate were not directly quantified in this study, data from nearby weather stations demonstrated that key aspects of climate differ at a regional scale between the range center and northeastern range edge. In both regions, *J. diphylla* primarily utilizes the early spring through early summer for growth and reproduction; plants often senesce for the year by mid-summer (Baskin & Baskin 1989; J. Bellemare, *personal observation*). As such, the length of the growing season *per se* does not appear to be a constraining factor for this species in either region (i.e., 1-2 months of mid- to late-summer are not utilized). Prior studies near the range center in Indiana have documented the potential for late frosts to impact fruit and seed set in *J. diphylla* (Smith et al. 1986); however, given the overall shift in the species' phenology from the range center to the range edge (i.e., later emergence and flowering in the north), it is not clear that the likelihood of late frosts would be different between the two regions. Notably, no large-scale failures of fruit set have been observed for the species near its northeastern range edge during the period of research associated with this study (2006-2009; J. Bellemare, *pers. obs.*). Indeed, the rate of inflorescence failure tended to be higher in the range center (Table 1.2).

The Biotic Environment

In contrast to abiotic factors, no significant associations were found between *J. diphylla* performance or population characteristics and aspects of the competitive environment (i.e., species richness and cover of other plant species; Table 1.4). Marginally significant negative correlations ($0.10 > p > 0.05$) were detected between the species richness of plots and *J. diphylla* cover, plant height, and potential seed production; however, this pattern seemed to be driven primarily by plots in which large, multi-ramet *J. diphylla* adults had high cover (e.g., 70-90%), apparently excluding other, smaller-statured plant species. As such, this pattern appeared to be driven primarily by the impacts of *J. diphylla* on other plant species, not vice-versa. Interestingly, plant species richness was found to be significantly lower in plots at the northeastern range margin (Table 1.4), but there was no evidence that this feature of the biotic environment correlated with *J. diphylla* performance or population structure within northeastern population sites, despite considerable variation in the species richness of plots within and between sites (Pearson correlation r p-value > 0.20 in all cases; results not shown).

Overall, these results suggest that variation in the competitive environment experienced by *J. diphylla* does not cause aspects of the species' performance or population structure, or directly explain regional differences in performance, in spite of the generally lower species richness at the northeastern range margin. This may be the result of two factors. First, although ecological theory has long predicted that higher species richness should produce more competitive, invasion-resistant communities (Elton 1958), recent studies in natural plant communities have raised questions about the relative importance or impact of species richness *per se* on competitive dynamics (Gilbert & Lechowicz 2005; Stohlgren et al. 2008). Second, field observations and the results of this study suggest that *J. diphylla* may be a superior competitor relative to most other forest understory plant species, at least within the narrow range of edaphic conditions that it typically occupies (i.e., high pH calcareous soils). Specifically, the relative importance of *J. diphylla* was > 10% in 14 of the 16 populations surveyed (~ 88%) and was > 25% in 6 of 16 populations (~ 38%), meaning that the species comprises a substantial proportion of total plant cover in these communities, in many cases being the most abundant understory plant species (J. Bellemare, *pers. obs.*). Given that the population sites occupied by *J. diphylla* appear to be located on some of the most nutrient-rich and productive upland forest soils in the regions investigated, the predominance of *J. diphylla* on these sites suggests that it may be near the top of the competitive hierarchy of such forest plant communities (Keddy & MacLellan 1990; Keddy et al. 2002). Consequently, competitive effects of other plant species on *J. diphylla* may be limited (Keddy 2007).

Unlike plant competition, there was clear evidence that another biotic factor, namely seed predation, differed between *J. diphylla* populations located in the species' range center and at the northeastern range edge. On average, 56% of the fruits in northeastern range edge populations were predated before they fully matured, while only 12% of fruits were predated in range center populations (Table 1.2). However, despite higher seed predation rates, the amount of seed successfully produced per m^2 in range edge populations tended to be greater than range center populations ($p < 0.10$) and the densities of seedlings and juveniles were comparable or somewhat higher in populations at the northeastern range edge (Table 1.2). Notably, prior studies of *J. diphylla* populations in West Virginia and Indiana have also documented high seed predation rates by rodents, including rates of fruit loss approaching 85-90% in some large populations (Heithaus 1981; Smith et al. 1986). This suggests that the impacts of this biotic factor are not restricted to the range edge.

The higher rates of seed predation documented by this study at the range edge likely traces to the substantially denser and more productive populations of *J. diphylla* located in this region when compared to the species' range center. This greater resource may be more apparent to individual seed predators and may also attract more seed predators due to the large numbers of fruits that ripen simultaneously in mid-June. The lower density and more limited production of fruits seen in range center populations may result in lower apparency to individual seed predators, as well as fewer seed predators being attracted to population sites. Field observations suggested that eastern chipmunks were responsible for much of the seed predation in northeastern range edge populations: chipmunks were frequently observed foraging in large populations, pulling down fruit stalks and opening matured fruits (J. Bellemare, *personal observation*). Notably, seed predation was less frequent or nearly absent in some range edge populations, despite the presence of chipmunks and large numbers of ripening fruits (J. Bellemare, *personal observation*). This might suggest a learned component to rodent foraging on this plant species near its range edge.

Because higher seed predation was the only factor found to differ between range center and range edge in a manner that might correspond to the determination of range limits, the potential for biotic limitation of the northeastern range edge needs to be considered. However, this possibility does not seem likely for two reasons. First, despite higher seed predation rates, seed production and the density of seedlings were comparable, if not higher, in range edge populations (Table 1.2). While seed production, and potentially seedling recruitment, is undoubtedly depressed by rodent seed predation, it does not appear to fall to levels that would explain the current position of the range edge. Second, rodent populations frequently exhibit cyclical patterns with inter-annual population spikes and crashes (Wolff 1996; Brooks et al. 1998). In the deciduous forests of eastern North America, these cycles often track mast years of oak (*Quercus* spp.; Wolff 1996; McShea 2000). As such, in years with low rodent densities following failed acorn crops, it is possible that seed predation rates in range edge populations of *J. diphylla* could be substantially lower, leading to seed production levels many times higher than those observed following high rates of fruit predation in 2007 and 2008 (Table 1.2). For a long-lived perennial plant species, these occasional years of substantially higher realized seed production would appear to be sufficient to overcome any biotic limitation on range expansion that seed predators might impose in other years, at least when averaged over the course of many decades or centuries.

Conclusions

The results of this study demonstrate that the distribution and abundance of *J. diphylla* near its range center and at its northeastern range edge follow a pattern inconsistent with abundant-center range models premised on species distributional equilibrium with the environment. Instead, evidence from surveys of population structure and individual performance document vigorous populations and large, productive individuals near the species' current northeastern range margin. Even as these findings demonstrate that highly suitable habitat for *J. diphylla* exists at the species' range margin, geologic evidence and field observations suggest that similar areas of suitable habitat may occur substantially beyond the species' current range edge in the Northeast (Bellemare et al. 2005; Bellemare 2009a).

While not well-described by an abundant-center range model, the patterns documented in this study are compatible with non-equilibrium range models predicting long-term time lags in migration and the potential for slow-moving colonization fronts in dispersal-limited plant species (Davis 1986; Holt et al. 2005; Gaston 2009). As an ant-dispersed forest plant with relatively limited seed production, *J. diphylla* appears to exhibit a number of the life history characteristics that may contribute to such limited dispersal and colonization ability (Verheyen et al. 2003; Van der Veken et al. 2007). In addition, the species' specialized edaphic niche (i.e., high pH soils) may result in a patchy distribution of potential habitat, further limiting colonization and migration potential (Hanski 1999; Matlack & Leu 2007).

In the context of the late Quaternary vegetational history of eastern North

America, the most plausible explanation for the distribution and abundance patterns exhibited by *J. diphylla* appears to be ongoing range expansion into a formerly glaciated region with suitable, but unoccupied, habitat. While the species' northeastern range margin has been static on historical timescales, as evidenced by herbarium records dating from the late 19th and early 20th century (Bellemare 2009a), the range edge may be expanding eastward and to the north on centennial to millennial timescales through rare, "nonstandard" dispersal events (i.e., not via ant-dispersal; Higgins et al. 2003). Range dynamics of this nature were likely ubiquitous among temperate forest plant species during the late Pleistocene and early Holocene, as species expanded their distributions from full glacial refugia, but the prospect that such range expansion might still be ongoing for some species is largely unexpected (Webb 1986; Cain et al. 1998; Clark 1998; Williams et al. 2001). Indeed, the results of the present study may provide some of the first field-based evidence for the existence of an eastern North American plant species with distribution and abundance patterns indicative of an ongoing, post-glacial range expansion (also see Holland 1980). A parallel study (Bellemare 2009a) is currently testing this possibility through experimental seed sowing beyond the current range margin of *J. diphylla* in the Northeast. Interestingly, the possibility of range dynamics of this nature is also becoming more apparent in the temperate forest flora of Europe (Svenning & Skov 2004; Svenning & Skov 2007; Van der Veken et al. 2007; Svenning et al. 2008), suggesting that long-term, dispersal-limited range dynamics may be more common than previously assumed. Clearly, the potential for migrational lags of this magnitude (e.g., centuries to millennia) has critical implications for developing conservation strategies in the face of rapid, anthropogenically-caused climate change in the present century (Bellemare 2009b).

Overall, the findings of this research, as well as those of other studies showing patterns at odds with standard abundant-center range models, suggest that ecologists need to reconsider conceptually attractive, yet overly simplistic, geographic range models. Instead, it may be necessary to develop more refined models that better incorporate the spatial complexities of geologic and edaphic factors and the potential for historical effects and dispersal limitation to impact present-day distributions. Such range models may be key to better understanding species' current geographic ranges and more accurately predicting species' responses to future environmental changes.

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CHAPTER 2

THE GEOGRAPHIC RANGE OF *JEFFERSONIA DIPHYLLA*, PART II: SEED DISPERSAL LIMITS THE LOCAL DISTRIBUTION AND GEOGRAPHIC RANGE OF AN ANT-DISPERSED FOREST PLANT SPECIES

Abstract

In this study we investigate the local distribution and geographic range edge of an ant-dispersed forest herb, *Jeffersonia diphylla,* to test whether the species' distributional limits in the northeastern United States may be limited by seed dispersal rather than contemporary environmental factors. Surveys of seedling and juvenile distribution relative to adult plants across 14 populations showed that the mean distance of young plants to adults is < 33 cm, with no seedlings or juveniles documented > 2.4 m. In contrast, experimental seed sowing along population margins demonstrated that suitable sites for seedling germination occurred at distances up to 100x the mean distance from naturally occurring seedlings to adult plants (~ 0.33 m vs. 30-50 m), indicating that the observed distribution of seedlings is significantly limited by seed dispersal on local scales. In a second seed sowing experiment, we found that highly suitable sites for seedling germination and growth occurred in areas up to 300 km beyond the species' current range margin. Indeed, seedlings at beyond-range sites grew significantly larger and transitioned to the juvenile life stage at a higher rate than seedlings growing at currently-occupied sites within the species' range. The study's results suggest that the local and large-scale distribution of *Jeffersonia diphylla* may be significantly limited by seed dispersal. Given the limited colonization rate inferred from seedling distributions in the field, it is possible that the species' current range margin in the Northeast represents a slow-moving, post-glacial colonization front

entering the region from the south.

Introduction

The nature and determinants of geographic range edges have figured prominently in ecological and evolutionary theories for many years (Mayr 1963; MacArthur 1972; Antonovics 1976; Hoffman & Blows 1994; Holt et al. 2005; Gaston 2009). Explanations for the current position and apparent stasis of many species' range edges commonly invoke an equilibrium between species' distributions and limiting features of the abiotic or biotic environment, as well as the restricted capacity of range edge populations to evolve in response to these factors and expand their distributions further (Hoffman & Blows 1994; Gaston 2003; Holt et al. 2005; Gaston 2009). Empirical and experimental studies of a number of plant species' distributions have demonstrated the key roles that such abiotic factors, ecological interactions, and evolutionary dynamics may play in determining the positions of range edges (e.g., Pigott & Huntley 1981; Carey et al. 1995; Nantel & Gagnon 1999; Angert & Schemske 2005; Geber & Eckhart 2005; Griffith & Watson 2006). Nevertheless, it is also apparent that species' geographic distributions do change over longer periods of time (e.g., centuries to millennia), often associated with long-term changes in environmental conditions (Huntley & Webb 1989). While these historical patterns ostensibly reinforce the connections between species' distributions and environmental factors (especially climatic conditions), they also highlight the potential for a qualitatively different form of range edge, namely non-equilibrial range margins generated by dispersal limitation (Davis 1986; Holt et al. 2005; Gaston 2009). Specifically, if rates of environmental change exceed the dispersal and colonization capacity of a species, current range edges may not correspond to limiting abiotic or biotic factors in the environment, but rather they may represent a stage in an ongoing range expansion contingent on species' dispersal rates (Davis 1986; Holt et al. 2005; Gaston 2009). While such non-equilibrial range edges may be most conspicuous in the case of exotic species with rapidly expanding invasion fronts, they are also conceivable for slowly-dispersing native species that may still be adjusting their distributions to past changes in the environment (Davis 1986; Holt et al. 2005; Gaston 2009).

Traditionally, climatic factors, rather than dispersal, have been viewed as central to limiting species' geographic distributions (Salisbury 1926; Webb 1986; Woodward 1987; Gaston 2003). The increasing evidence that the range edges of many species have already begun to shift poleward in response to anthropogenic climate change is consistent with this view (e.g., Parmesan & Yohe 2003; Parmesan 2005; Hickling et al. 2006). At the same time though, other studies have found evidence that other species' distributions may still be restricted due dispersal limitation and long-term time lags in range expansion following episodes of past climate change (e.g., Pleistocene glaciation; Van der Veken et al. 2007a; Svenning & Skov 2007; Svenning et al. 2008). Taken together, these varied findings on the contemporary and historical causes of species' distributions suggest that there may be a broad continuum of geographic range dynamics, from 'fast' species with the capability for rapid range adjustments in response to environmental change (c.f., 'dynamic equilibrium'; Webb 1986), to 'slow' species with substantially more limited migration rates and the potential for large-scale range disequilibrium with the contemporary environment (Davis 1986; Holt et al. 2005; Van der Veken 2007a; Svenning & Skov 2007). Gaining a clearer understanding of the traits and ecological characteristics that may drive these divergent possibilities will be key to developing more accurate geographic range models (Bellemare 2009a), as well as to identifying species most imperiled by rapid climate change (Van der Veken et al. 2007a;

Bellemare 2009b).

One of the principal challenges to understanding the potential for non-equilibrial range dynamics is further resolving the relationship between local- and long-distance dispersal. While local dispersal dynamics have often been investigated in empirical studies, allowing for direct estimates of local dispersal patterns (Howe & Smallwood 1982; Cain et al. 1998; Gomez & Espadaler 1998), long-distance dispersal has generally eluded direct empirical research due to its rarity and unpredictability (Higgins et al. 2003a; Higgins et al. 2003b; Nathan 2006). Nevertheless, theoretical analyses suggest that it is just such rare, long-distance dispersal events that are key to determining plant migration rates and patterns of range expansion (Cain et al. 1998; Clark 1998; Higgins et al. 2003a; Nathan 2006). Further complicating the issue, a number of studies have highlighted the apparent disconnect between local dispersal dynamics and long-distance dispersal, noting that rare long-distance dispersal events occur under unusual circumstances and by 'nonstandard' means (Cain et al. 1998; Higgins et al. 2003a; Nathan 2006). As such, the mean dispersal distance achieved via 'standard' dispersal modes may be far less important in determining migration rates than the few extreme outliers resulting in colonization of areas beyond current range edges (Cain et al. 1998; Clark 1998; Nathan 2006). Consequently, studies that have documented correlations between standard dispersal modes, as defined by seed morphological traits, and local dispersal patterns may be of ambiguous value for understanding large-scale geographic range dynamics (Matlack 1994; Cain et al. 1998; Clark 1998; Bellemare et al. 2002; Higgins et al. 2003a; Nathan 2006).

Even so, a limited number of comparative studies have found evidence of correlations between dispersal-related aspects of seed morphology and geographic range size, suggesting that trait-based information on species' seed dispersal modes and data on local dispersal patterns may be relevant to studies of long-distance dispersal and large-scale range dynamics (Edwards & Westoby 1996; Lloyd et al. 2003; Van der Veken et al. 2007a). These studies have documented that plant species with seeds exhibiting adaptations for dispersal by wind or vertebrates, or those with a greater relative investment in these traits, often have larger geographic ranges than related species without these adaptations or with less investment in these traits (Edwards & Westoby 1996; Lloyd et al. 2003; Van der Veken et al. 2007a). For example, Van der Veken et al. (2007a) found that forest plant species with seeds adapted to small-scale dispersal by ants and those with no obvious adaptations for dispersal had significantly smaller distributions in western Europe than related species with wind- or vertebrate-dispersed seeds. These and other studies make clear that investigation of local dispersal dynamics may still offer insights to understanding long-distance dispersal and range expansion processes (Van der Veken et al. 2007a; Bullock & Nathan 2008; Soons & Bullock 2008). Indeed, such insight may be a critical complement to theoretical studies grappling with essentially unobservable, rare events like long-distance dispersal (Bullock & Nathan 2008).

In this study, I investigated the local distribution and geographic range margin of *Jeffersonia diphylla*, an ant-dispersed forest plant species, to ask whether dispersal limitation at local scales may translate to dispersal limitation of geographic range margins. Do local dispersal dynamics help to explain the nature of the species' geographic range edge, or are these two processes unrelated due to the oft-cited disconnect between local dispersal patterns and rare long-distance dispersal events? Additionally, can a species be dispersal-limited on local scales, but still exhibit a distribution in dynamic equilibrium with the environment on large geographic scales? *J. diphylla* presents an ideal species to investigate these dispersal-related dynamics for several reasons. First, the species exhibits a number of the life history characteristics that have been linked to dispersal limitation at local scales, such as ant-dispersed seeds and limited seed production (Verheyen et al. 2003; Mabry 2004). Second, prior research by Bellemare (2009a) has demonstrated that population- and individual-level performance of *J. diphylla* do not decline toward its northeastern range edge. This pattern suggests that non-equilibrium range dynamics are plausible for the species (Bellemare 2009a). Finally, *J. diphylla* has a well-defined edaphic niche centered on calcium-rich, circumneutral soils (Gleason & Cronquist 1991; Bellemare 2009a); this characteristic makes the identification of potentially suitable habitat beyond current range margins feasible, allowing for a clear test of dispersal limits on the species' current range edge.

To assess the relative importance of dispersal limitation at local and regional scales, I utilized a three-tiered approach combining descriptive and experimental methods: First, I conducted field surveys of seedling and juvenile distribution relative to adult plants to document evidence of dispersal dynamics in natural populations of *J. diphylla*. Second, I established experimental seed sowing plots along transects running from adjacent to adult plants into nearby unoccupied habitat to test for local dispersal limitation. Finally, I used experimental seed sowing at sites within and beyond the range edge of *J. diphylla* in the northeastern United States to test for large-scale dispersal limitation of the species' range edge in the region. Taken together, these approaches should provide a comprehensive, multi-scale test of the role that dispersal limitation plays in determining the local distribution and geographic range edge of *J. diphylla*.

Methods

Study Species

Jeffersonia diphylla (Berberidaceae) is a long-lived, perennial herb native to the temperate deciduous forests of eastern North America (Gleason & Cronquist 1991;

George 1997). Adult plants typically occur as a single ramet or in larger, multi-ramet clumps. Each ramet includes between 2-17 leaves and can produce a single white flower in early spring (Smith et al. 1986). Seeds are produced in a capsule that dehisces on the plant when ripe, dropping between ~ 20-40 seeds on the ground below the plant (Gleason & Cronquist 1991; J. Bellemare, *personal observation*). The seeds include a fleshy, lipid-rich attachment (elaiosome) that is attractive to ants, often resulting in the seeds being collected and dispersed by foraging ants (myrmecochory; Heithaus 1981; Smith et al. 1986). *Jeffersonia diphylla* ranges from northwestern Georgia and northeastern Alabama, north to central New York, southern Ontario, and southeastern Minnesota (Gleason & Cronquist 1991; George 1997). Throughout its range, *J. diphylla* is closely associated with circumneutral, calcareous soils in the vicinity of limestone or other carbonate-rich bedrocks (Gleason & Cronquist 1991; Bellemare 2009a).

Seedling and Juvenile Distribution Relative to Adult Plants

To assess evidence of local seed dispersal patterns, the distribution of seedlings and juveniles relative to adult plants was assessed in 14 natural populations of *J. diphylla* in Kentucky, Ohio, Indiana, and New York (population locations listed in Appendix). In randomly placed 0.5 x 0.5 m quadrats, I measured the distances from all seedlings and juveniles encountered to the nearest adult *J. diphylla*. From these data, the mean distances from adult plants to seedlings, and from adults to juveniles, were calculated and the general form of the distribution x density relationship was assessed using Goodness-of-Fit tests in JMP 7.0.2 (SAS Institute, Cary, NC).

Seed Sowing Experiment I: Is the local distribution of Jeffersonia diphylla *limited by seed dispersal?*

To experimentally test whether the natural distribution of *J. diphylla* seedlings relative to adult plants was influenced by dispersal limitation, experimental seed sowing plots were established along 40-50 m transects running from adjacent to adult plants out into unoccupied habitat at three population sites in central New York in June 2008. Three to four transects were established at each site, with 10 transects in total across the three research sites. Experimental plots along each transect measured 0.25 x 0.25 m in size. In each plot, the soil surface was lightly disturbed with a pocketknife and 20 seeds were pressed into the mineral soil to a depth of ~ 1 cm; the locations of individual seeds were not marked within the plots. Seeds for each experimental site were collected from within the local population; in particular, all ripening fruits on plants growing adjacent to the start of the transects were collected and used in order to minimize the possibility of natural seed dispersal into the experimental plots.

Experimental plots were established at higher density along the start of the transects (i.e., near adult plants), as preliminary field observations suggested that naturally occurring seedlings peaked in abundance close to sexually-reproductive adults. As such, it was deemed necessary to have greater resolution on seed germination rate x distance relationships in the first meters around adult plants. Plots were established each 0.5 m from 0 to 3 m from adult plants, at 1 m intervals from 3 to 10 m from adult plants, and at 5 m intervals from 10 to 40 or 50 m from adult plants. In total, eight 50 m transects (22 plots each) and two 40 m transects (20 plots each) were established; the shorter transects were located in positions where a stream or logging road compromised the area beyond 40 m.

In May 2009, seed plots along the transects were surveyed for the number of seedlings that had emerged. Trends in germination rate x distance from adult plants were assessed for each transect individually, as well as for mean site-level patterns. Correlations between germination rate and distance were analyzed with linear regression in JMP 7.0.2.

Seed Sowing Experiment II: Is the geographic range of Jeffersonia diphylla *limited by seed dispersal?*

To experimentally test the possibility that the geographic range of *J. diphylla* is limited by seed dispersal, seeds were sown in experimental plots within and beyond the species' range edge in the northeastern United States and germination, survival, and growth were compared. Seed plots for this experiment were established at 3 population sites within the species' range in central New York and at 3 unoccupied, but seemingly suitable, sites beyond the species' range in western Massachusetts.

As this experiment was predicated on the nature and location of the range edge of *J. diphylla* in the Northeast, it is important to clearly define the 'range edge' used in this study and to identify its geographic position relative to the study sites located 'beyond' the species' range edge. Standard botanical references place the northeastern range edge of *J. diphylla* in central New York, with outlying populations noted on the north side of Lake Ontario in Canada (Figure 2.1; Gleason & Cronquist 1991; George 1997). This delineation is based on the occurrence of between 25-30 extant and historical *J. diphylla* populations in central and western New York, many including 100s to 1000s of plants (Weldy & Werier 2009; Bellemare 2009b; C. Sheviak, *personal communication*). At a coarse geographic scale, the area of central and western New York occupied by these populations is roughly contiguous with regions occupied by *J. diphylla* in northern Ohio, and the rest of the species' geographic range in the Midwest and Southeast (George 1997). In the context of this study though, two outlying records of *J. diphylla* in the Northeast deserve note. First, a historical record

(1883) for the species is known from Westchester County in southeastern New York, although this site has apparently not been documented since the late 19th century (Figure 2.1; Weldy & Werier 2009). Second, in April 2000, a small *J. diphylla* occurrence, including just 9 individuals, was discovered in Rensselaer County in the Hudson River Valley of eastern New York (Weldy & Werier 2009); this new site is located ~ 200 km east of the easternmost extant population of the species near Syracuse, New York (Figure 2.1). The history and origin of the new Rensselaer County population are unknown: it may represent a relict of a larger population formerly located in the area, the outcome of a recent long-distance colonization event, or a naturalization or escape from cultivated *J. diphylla* plants.

In the present study, the experimental sites located 'beyond' the range edge of *J. diphylla* are situated in an area in western Massachusetts located ~ 300 km east of the primary range edge in central New York, ~ 200 km northeast of the historical record in Westchester County, New York, and ~ 100 km east of the new occurrence record in Renssalear County, New York (Figure 2.1). Natural populations of *J. diphylla* have never been documented in Massachusetts or other New England states (Gleason & Cronquist 1991; Sorrie & Somers 1999; Magee & Ahles 2007). As such, regardless of how the northeastern range margin of *J. diphylla* is defined, the experimental sites were a substantial distance (i.e., ~ 100 to ~ 300 km) outside the species' natural geographic distribution in the northeastern United States.

The within-range, 'control' sites for this experiment were located in three naturally-occurring *J. diphylla* populations in Cayuga and Onondaga Counties in central New York (Figure 2.1). Because selection of treatment sites beyond the range edge could not be guided by such natural occurrences of *J. diphylla* (i.e., to indicate site suitability for the species), several environmental and botanical features were used as guides for site suitability. First, based on the species' known preference for

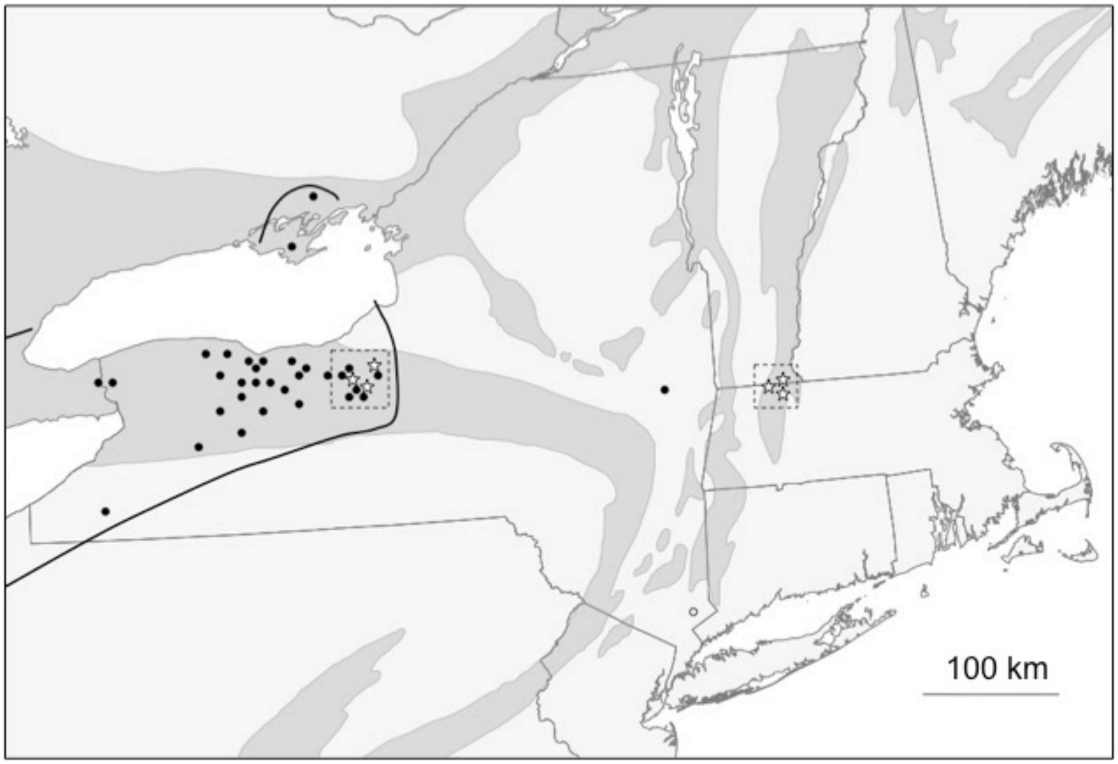

Figure 2.1. The northeastern range edge of *Jeffersonia diphylla* relative to the generalized occurrence of calcareous bedrock types in the region. The standard range margin for the species is indicated by a heavy black line in the left portion of the figure. The locations of historical and extant populations are indicated with black points; calcareous bedrock is indicated by gray shading. A 19th century occurrence record from Westchester County in southeastern New York is indicated by a hollow circle positioned near the center of the county. A recently discovered occurrence of 9 plants in Rensselaer County in eastern New York is indicated, but not included within the standard range margin. The locations of the three within-range study populations in central New York are indicated by stars and a dashed line box; the locations of the three beyond-range study sites in western Massachusetts are indicated by stars and a dashed line box. The locations of populations are approximate, as the figure is based in part on a hand-drawn map housed at New York State Botanist's office at the New York State Museum, Albany, NY.

calcareous soils (Baskin & Baskin 1989; Gleason & Cronquist 1991), sites in western Massachusetts that were documented to have calcium-rich, circumneutral soils were identified using soils data from prior research by the author (Bellemare et al. 2005). Second, sites were selected that supported populations of other 'calciphile' plant species that were commonly found growing with *J. diphylla* within its range (e.g., *Actaea pachypoda*, *Adiantum pedatum*, *Asarum canandense*, and *Caulophyllum thalictroides*). Third, sites were located on east to southeast facing slopes with mesic soils, similar to the setting of the control sites in central New York. Overall, this resulted in a relatively close matching of abiotic and biotic environmental conditions at the treatment and control sites. Specifically, the control sites were characterized by *Acer saccharum*-dominated forest canopies, a species-rich herbaceous layer including calciphile-type plant species, and nutrient-rich soils over calcareous bedrock (e.g., limestone, dolomite, or calcareous shale). The three 'treatment' sites located beyond the range edge of *J. diphylla* were also situated in *Acer saccharum*-dominated forests including calciphile-type plant species, on nutrient-rich soils over calcareous bedrock (e.g., calcitic marble).

Following initial site selection, the environmental similarity of the control and treatment sites was further quantified. Slope and aspect were measured at several points within each site, and elevation was determined from United States Geological Survey (USGS) topographical maps. To characterize edaphic conditions at each site, four soil samples (0-10 cm depth) were collected for chemical and physical analyses; these soils were dried and sieved prior to analysis, as described in Bellemare (2009a). Soil samples from within each site were pooled and homogenized, and a subsample from each site was analyzed for soil texture, organic matter content, pH, and cation concentrations at Brookside Labs (New Knoxville, OH). To assess basic climatic conditions in the two study areas, data on average monthly temperatures and precipitation (1971-2000) were compiled from the CLIMOD database (http://climod.nrcc.cornell.edu) from four weather stations located in the vicinity of the study sites in each region (< 50 km). For precipitation, summed values for April through July were determined, as this is the primary growing season for *J. diphylla* in the Northeast (Bellemare 2009a). While limited sample size precluded statistical analysis of these environmental data (i.e., N = 3 within-range and 3 beyond-range sites), they should provide some insight to general environmental similarities and differences between the two regions (Table 2.1).

The *J. diphylla* seeds used in this experiment were collected from natural populations located at the control sites in central New York. Seeds were collected in late June 2006 as fruits had ripened and begun to dehisce. Seeds were manually removed from the fruits and sorted onto moistened filter paper in covered Petri dishes. Seeds were held at ambient outdoor temperatures for up to 1 week prior to planting in the field in late June and early July 2006.

Only seeds from the local population were planted at the control sites within the range. At the treatment sites beyond the range, seeds from 2 of the 3 control sites were used in a 50:50 mixture; sufficient seed from the third control site was not available for use at treatment sites due to heavy seed predation by rodents in late June 2006. At each control site, between 5 and 18 experimental plots measuring 0.5 x 0.5 m were haphazardly established within the *J. diphylla* population area. The number of plots established at control sites was determined by seed availability in the local population after seeds had been allocated to treatment sites. The spatial distribution of control plots was adjusted as the plots were established so as to not include mature *J. diphylla* plants; the mean distance from the plots to mature plants was 1.9 m (SE ± 0.4), with a range from 8 cm to 9.9 m. Plant species growing in the plots were left undisturbed. Twenty seeds were planted in each plot following a 10 x 10 cm grid;

each seed was lightly pressed into the soil to a depth of ~1 cm. The location of each seed was marked by a segment of colored wire inserted into the soil. At the three treatment sites beyond the range edge, 14 experimental plots were established at each site following the same protocol used within the range. In total, 37 plots with 740 seeds were established at the 3 control sites within the range, and 42 plots with 840 seeds were established at the 3 treatment sites beyond the range edge. All plots were revisited in late summer 2006 to confirm that rodent seed predation or other disturbance had not compromised the plots subsequent to establishment; no signs of seed predation or disturbance were observed.

Germination rate, based on the number of seedlings emerging, was measured between May 11-15th, 2007. Importantly, all seeds planted in June 2006 that survived until spring 2007 should have germinated at this time, as seeds of *J. diphylla* exhibit deep, simple morphological dormancy (Baskin & Baskin 1989). This means that seeds germinate following a single warm-cold cycle (Baskin & Baskin 1989). As such, *J. diphylla* does not form a persistent soil seed bank. In addition to *J. diphylla* germination, each plot was assessed for species richness (# of plant species rooted in plot, excluding the experimental plants), cover (%) of the herbaceous layer (vascular plants < 1 m), and cover (%) of leaf litter on the soil surface. Soil cores (0-10 cm depth) were collected immediately adjacent to each plot and assessed for bulk density following the protocol described in Bellemare (2009b); subsamples of each soil core were analyzed for soil pH by Brookside Laboratories, Inc. (New Knoxville, OH).

In June 2008, the experimental plots were re-surveyed to assess survival of the *J. diphylla* seedlings that had emerged in spring 2007. In addition, life stage transitions from seedling to juvenile (1 to 2 leaves) were recorded and leaf area was quantified by tracing leaves onto note cards. The leaf traces were then cut out and scanned to determine leaf area (cm^2) on a LI-COR 3100 Area Meter (LI-COR

Environmental, Lincoln, NE). The cover of the herbaceous layer and leaf litter, and the species richness of plots were also re-surveyed at this time.

Differences in seed germination rates, seedling survival rates (through June 2008), and seedling leaf size (in June 2008) were related to region (within vs. beyond range) and site using ANOVA, with site nested within region. In addition, a series of exploratory regression analyses and ANOVA were conducted to evaluate associations between seedling performance metrics and characteristics of the abiotic and biotic environment in the experimental plots, including soil bulk density, soil pH, plant species richness, and cover (%) of the herbaceous layer and leaf litter. Due to substantial within-site heterogeneity of the biotic and abiotic environment among plots (e.g., range of 10 to 80% herbaceous layer cover and soil pH from 4.8 to 7.4 among plots at individual sites), these exploratory analyses were conducted on individual plot values, rather than site averages. While the individual plots cannot be considered true independent replicates, treating them as such in these analyses may provide useful insight to the effects of the abiotic and biotic environment on the germination and establishment of *J. diphylla*. All seed and seedling analyses were conducted in JMP 7.0.2.

Results

Seedling and Juvenile Distribution Relative to Adult Plants

In June 2008, 123 seedlings were encountered in quadrats sampled at the 14 *J. diphylla* populations surveyed. The mean distance from seedlings to the nearest *J. diphylla* of sexually-reproductive size was 33.4 cm (± 3.3 SE), with a range from 3 to 165 cm; random sampling extended to ~ 10 m from adult plants, but no seedlings were observed > 165 cm (Figure 2.2). The density x distance distribution of seedlings followed an approximately log-normal distribution, with the majority of seedlings

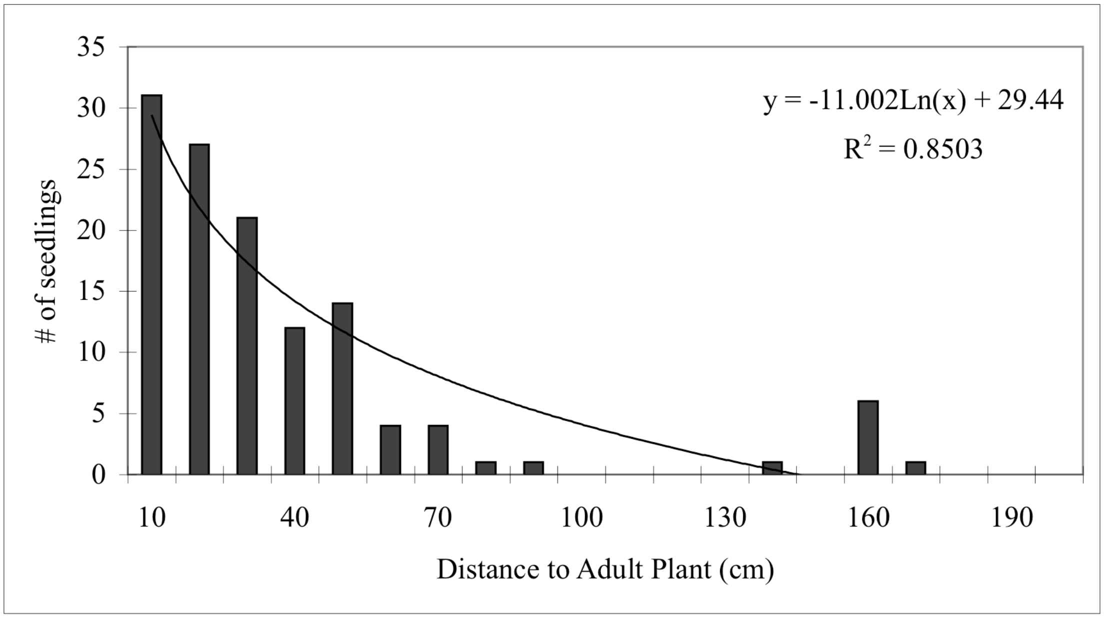

Figure 2.2. The distribution of 123 *Jeffersonia diphylla* seedlings relative to adult plants across 14 populations in Kentucky, Indiana, Ohio, and New York. The trendline represents a logarithmic function that describes the decline in abundance for the ~ 93% of seedlings that occurred less than 1 m from adult plants (i.e., distribution is log-normal); 6 of the 8 'outlier' seedlings documented beyond 1 m were located in a single plot in the remains of an ant nest. Sampling included 367 0.5 x 0.5 m plots and extended to ~ 10 m from adult plants, but no seedlings were documented beyond 165 cm.

concentrated near adult plants and a long "tail" with few, relatively extreme values far from adult plants; a goodness-of-fit test employing Kolmogorov's D did not reject the null hypothesis that the data were from a log-normal distribution ($p > 0.15$). Only 8 seedlings were documented > 100 cm from an adult plant, and 6 of these 8 were located in a single plot in what appeared to be the remains of an ant nest in rotted wood (J. Bellemare, *personal observation*). Notably, the distribution of seedling distances to adult plants is not significantly different from the distribution of fruit stalk lengths (mean 30.5 cm), as measured on 100 plants at 5 population sites (Welch ANOVA $p = 0.3805$).

In addition to the 123 seedlings, 88 juvenile plants were also recorded in the quadrats. Juveniles showed a distribution pattern similar to seedlings, with most juveniles concentrated near adult plants (mean distance: 22.7 cm ± 3.2 SE); juvenile distances ranged from 3 to 240 cm from adult plants, although sampling extended to ~ 10 m beyond adult plants. The density x distribution data for juveniles were also well fit by a log-normal distribution, with the majority of juveniles concentrated close to adult plants and a few individuals occurring at relatively extreme distances (Kolmogorov's D $p > 0.15$).

Seed Sowing Experiment I: Is the local distribution of Jeffersonia diphylla *limited by seed dispersal?*

In total, 583 seeds germinated from seeds planted along transects from adjacent to adult *J. diphylla* plants to nearby unoccupied habitat. The seedlings emerged in plots at all distances along these transects, from adjacent to adult plants (0-25 cm) to 50 m from adult plants. Seed germination rates varied between the three sites: at two sites seed germination occurred at moderate levels (16% and 24%, or 273 and 308 seedlings, respectively), whereas, the third site had low seed germination (<< 1%).

The cause of the very low germination is unclear, as seeds planted in other experimental plots at this site in 2006 for germinated at much higher rates (~ 26%; Seed Sowing Experiment II, described below).

Trends in germination rate x distance from adult plants were only analyzed for the two sites where substantial numbers of seedlings emerged in the experimental plots. These sites accounted for 581 of the 583 seedlings, and included 7 transects in total. At the first site, seed germination rate did not decline or increase significantly along any of the four transects. Averaged across the four transects, there was no evidence of any overall linear trend in germination rate with distance from adult plants ($p > 0.50$, $R^2 = 0.02$; Figure 2.3). At the second site, germination rate did not change significantly across any of the 3 individual transects ($p > 0.10$ in all cases), but the mean response across all three transects showed a marginally significant decline with distance ($p = 0.06$, $R^2 = 0.17$; Figure 2.3). However, the strength of this decline was modest: the germination rate averaged 6% higher in first 10 m of these transects than in the range from 15-50m (26% vs. 20%, respectively). Overall, it is of note that this experiment led to the appearance of 484 *J. diphylla* seedlings at distances from adult plants greater than that observed for any naturally occurring seedling documented in this study (i.e., distances > 165 cm).

Seed Sowing Experiment II: Is the geographic range of Jeffersonia diphylla *limited by seed dispersal?*

Basic environmental conditions were generally similar between the research sites within and beyond the range edge of *J. diphylla* in the Northeast. Of the climatic, physiographic, and edaphic factors considered, only soil texture and bulk density showed trends toward substantial differences, with soils at sites beyond the range edge being less dense and having more sand and less clay and silt (Table 2.1).

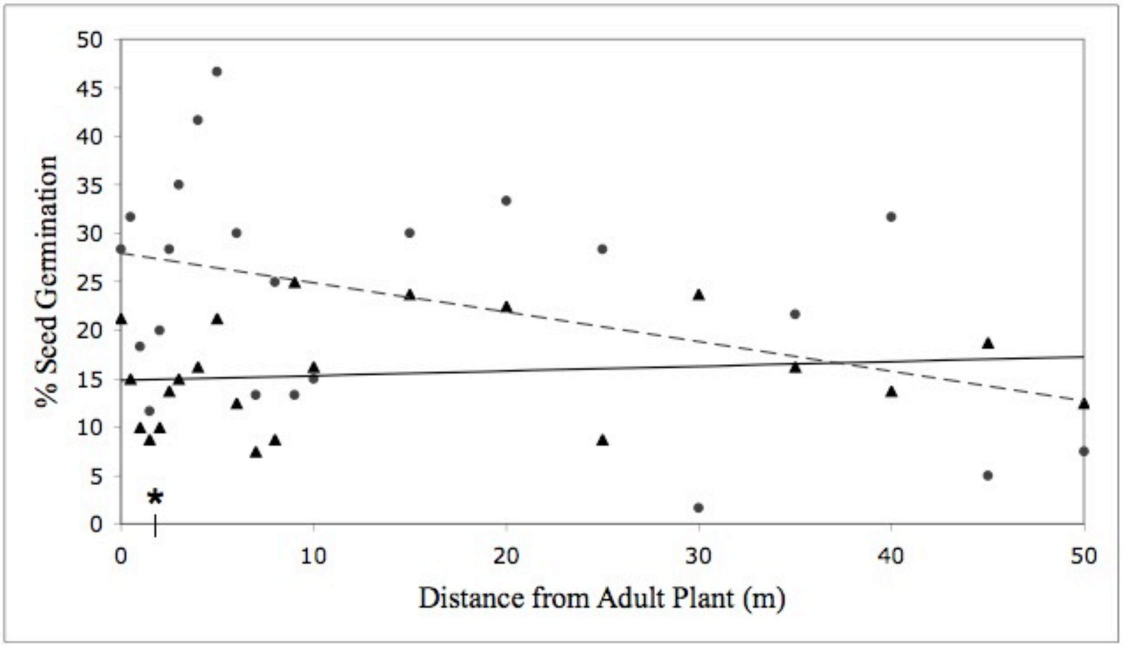

Figure 2.3. Mean seed germination rate (%) in experimental plots relative to distance from adult *Jeffersonia diphylla* plants at two population sites in central New York. Data represent the average response across four 50 m transects at Railroad Mills site (black triangles and solid line) and across two 50 m and one 40 m transect at Great Gully site (gray circles and dashed line). Seed germination was << 1% at a third site; data from the site are not depicted in this figure. Linear regression showed no significant correlation ($p > 0.50$; $R^2 = 0.02$) between distance and germination rate at the Railroad Mills site (black symbols) and a marginally significant negative correlation ($p = 0.06$; $R^2 = 0.17$) between distance and germination rate at the Great Gully site (gray symbols). The vertical black dash and asterisk on the left side of the x-axis mark the distance of the furthest natural occurrence of a *Jeffersonia diphylla* seedling from an adult plant documented in this study (i.e., ~ 165 cm; see Figure 2.2). Sample sizes: four transects with 88 plots and 1760 seeds at Railroad Mills; three transects with 64 plots and 1280 seeds at Great Gully.

Table 2.1. Abiotic environmental characteristics of experimental seed sowing sites within and beyond the geographic range of *Jeffersonia diphylla* in the northeastern United States. Values presented are means ± standard error. Soil pH and bulk density were measured for each plot individually; differences between sites and regions were tested with ANOVA with site effect nested in region. Significant effects of region are indicated by asterisk for these two variables: significance level for region effect is indicated by asterisks (*** = $p < 0.0001$). Other abiotic factors were only quantified at the site level making statistical analysis infeasible (i.e., N = 3 sites in each region). Climatic averages cover the period 1971-2000 and are based on data from 4 weather stations in each study area accessed through the CLIMOD database.

Abiotic Factor	**Within-range Sites**	**Beyond-range Sites**
Plot-level measures:		
Soil pH	5.9 ± 0.5	6.0 ± 0.2
Soil bulk density (g/cm^3)***	0.78 ± 0.16	0.62 ± 0.01
Site-level measures:		
Site slope (°)	18 ± 6	29 ± 1
Site aspect (°)	137 ± 33	129 ± 3
Elevation (m)	201 ± 44	263 ± 15
Soil texture: sand %	39.3 ± 3.8	75.6 ± 1.0
Soil texture: silt %	48.2 ± 1.6	23.8 ± 1.0
Soil texture: clay %	12.5 ± 3.1	0.7 ± 0.1
Soil organic matter %	8.7 ± 1.6	9.8 ± 0.7
Soil calcium (parts per million)	3067 ± 133	2989 ± 273
Mean annual temperature (°C)	8.3 ± 0.3	7.9 ± 0.4
Mean January temperature (°C)	- 5.3 ± 0.3	- 6.0 ± 0.3
Mean July temperature (°C)	21.3 ± 0.3	21.0 ± 0.5
Mean precipitation April-July (cm)	35.3 ± 0.7	41.6 ± 0.9

In total, 542 *J. diphylla* seedlings emerged from the 1580 seeds planted in the experimental plots within and beyond the species' natural range edge in the Northeast (~ 34% overall germination rate). Of the 542 seedlings, 507 (~ 94%) were first detected in the May 2007 plot survey, while the remaining 35 seedlings (~ 6%) were first observed in the June 2008 plot survey. Because *J. diphylla* seeds typically germinate after a single cycle of warm – cold stratification (Baskin & Baskin 1989), it is believed that the 35 'new' seedlings observed in June 2008 actually emerged in 2007, after the mid-May survey had been conducted.

Seed germination rate varied significantly between sites within and beyond the range edge: the germination rate was over 2 times higher at sites beyond the range edge than at naturally occupied sites within the range (21% vs. 48% germination, $p < 0.0001$; Table 2.2). The effect of site, nested within region, was also significant ($p = 0.0167$), although the mean germination rate was relatively high at all sites beyond the range edge (44, 50, 51%) and lower at all sites within the range (11, 25, 27%; Table 2.2).

Germination rates were significantly correlated with several features of the abiotic and biotic environment at the plot scale. A significant quadratic relationship was evident between soil bulk density (g/cm^3) and germination rate ($R^2 = 0.38$, $p < 0.0001$; Figure 2.4), with germination rate relatively low in low bulk density soils (~ 0.37 – 0.50 g/cm^3; mean germination rate = 32%), relatively high in soils of moderate bulk density (0.50 – 0.90 g/cm^3; germination rate = 44%), and very low in dense, high bulk density soils (0.90 – 1.28 g/cm^3; germination rate = 9%). A significant quadratic relationship was also detected between soil pH and germination rate ($R^2 = 0.19$, $p < 0.001$; Figure 2.5). Soil pH and soil bulk density were not strongly correlated ($R^2 = 0.02$, $p > 0.20$), suggesting that the relationships are relatively independent phenomena. Average germination rate was low at low pH (~ pH 4.8-5.5; mean

Table 2.2. Performance of *Jeffersonia diphylla* seeds sown at sites within and beyond the species' range edge in the northeastern United States. Values are means ± standard error. Significance values are based on f ratios for each effect (region, site). Germination and survival rate data were arcsine-square root transformed prior to analysis; total leaf area and leaf area were natural log transformed prior to analysis to equalize variances.

	Within Range	Beyond Range	Site Effect p value	Region Effect p value
Germination rate (%)	20.9 ± 5.1	48.4 ± 2.4	**0.0167**	**< 0.0001**
Survival rate to June 2008 (%)	8.6 ± 3.9	10.7 ± 3.4	**< 0.0001**	0.9510
Total leaf area per plant (cm^2)	6.1 ± 0.2	10.0 ± 1.4	0.2254	**0.0001**
Leaf area (cm^2)	6.0 ± 0.2	8.9 ± 1.0	0.1843	**0.0008**

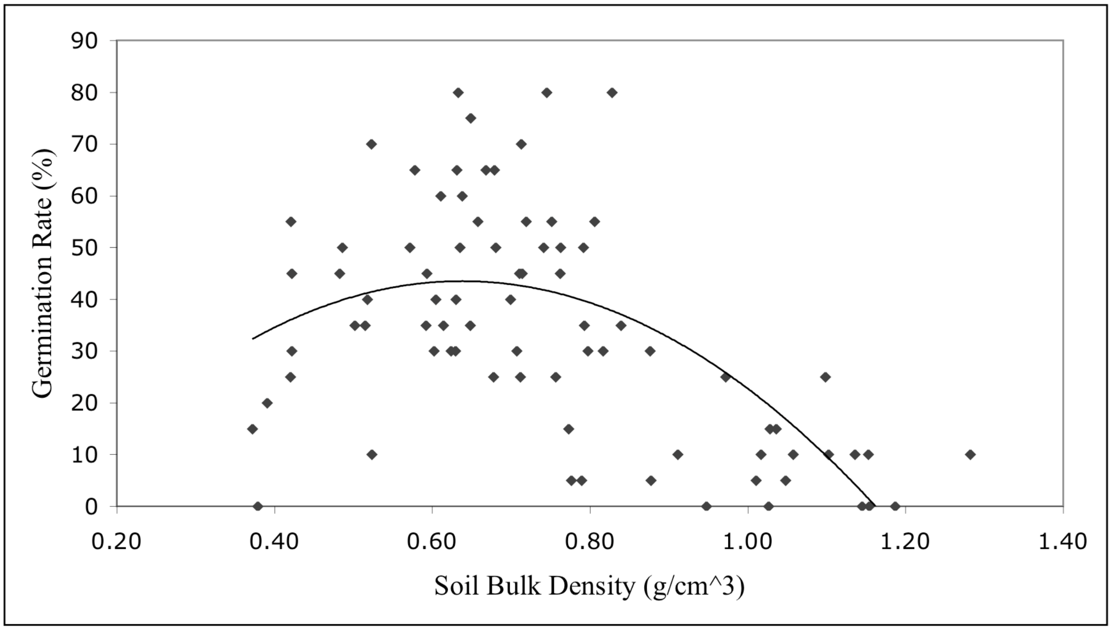

Figure 2.4. Germination rate of *Jeffersonia diphylla* seeds in relation to soil bulk density. The data depicted are untransformed, although quadratic regressions were run on transformed values: germination data were arcsine-square root transformed and bulk density values were natural log transformed prior to analysis. Data from 79 plots at 6 sites planted with 1580 seeds total.

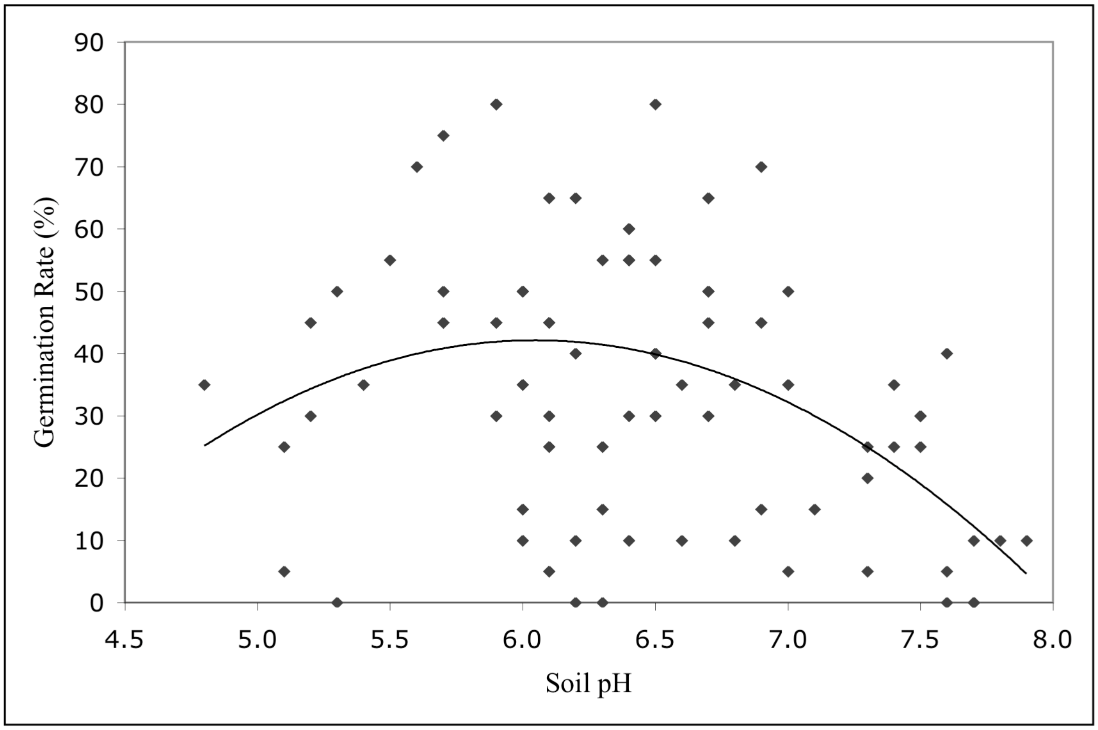

Figure 2.5. Germination rate of *Jeffersonia diphylla* seeds in relation to soil pH. Germination rate data depicted figure are untransformed, although quadratic regressions were run on arcsine-square root transformed values. Data from 79 plots at 6 sites planted with 1580 seeds total.

germination rate = 31%) and at high pH (~ pH 7.0-7.9; germination rate = 19%), with a peak in germination around pH 6 (pH 5.5 – 7.0; germination rate = 41%; Figure 2.5). Also, a significant positive correlation was detected between herb layer cover in experimental plots and germination rate ($R^2 = 0.14$, $p < 0.001$); no significant relationships were apparent between germination rate and species richness or leaf litter cover in the plots.

Of the 542 seedlings documented in the plots between 2007 and 2008, 154 (28%) survived into the second growing season (June 2008). The rate of seedling survival was higher at sites within the range compared to sites beyond the range edge: 64 of the 136 seedlings (47%) in within range plots survived into the 2008 growing season, while 90 of the 406 seedlings (22%) in beyond range plots survived into the 2008 growing season. However, given the significantly higher initial germination rate at sites beyond the range edge, the lower survival rate of seedlings in this region led to within and beyond range sites having similar percentages of seeds resulting in seedlings alive in June 2008. (9% and 11%, respectively; Table 2.2). In contrast to the results for germination rate, which was relatively uniform among sites within regions, but differed significantly between the two regions, the effect of site on survival was significant ($p < 0.0001$), while the effect of region was not ($p = 0.9363$; Table 2.2). For both regions, 2 of the 3 sites in each region had relatively high survival (13-15%) and 1 site in each region had relatively low survival (3-4%).

The growth rate of seedlings at sites beyond the range edge, as measured by total leaf area (cm^2) in June 2008, was significantly greater than the growth rate of seedlings within the range (beyond-range mean total leaf area = 10.0 cm^2, within-range mean total leaf area = 6.1 cm^2, $p < 0.0001$); the effect of site on growth rate was non-significant (Table 2.2). The significantly higher growth rate observed beyond the range edge was driven in part by the higher percentage of experimental plants in this region transitioning from the single-leaved ‘seedling’ life stage to the two-leaved ‘juvenile’ life stage (15.6% of plants); at sites within the range, only 3.1% of the experimental plants made this transition by June 2008. However, even after controlling for plants with two leaves and considering only area *per leaf*, the leaves of experimental plants beyond the range edge were significantly larger than the leaves of plants within the range (8.9 vs. 6.0 cm^2, respectively; $p < 0.001$; Table 2.2).

As with seed germination rate, several aspects of the abiotic and biotic environment were associated with the survival and growth of experimental plants through June 2008. Survival rate per plot exhibited a non-normal distribution due to the high percentage (38%) of plots exhibiting 0% survival. To analyze these data, survival rate was transformed to a categorical variable with three classes: 0% survival, low survival (5-10%; 23 plots), and high survival (> 10%; 26 plots); no plots had higher than 35% survival. One-way ANOVA was used to test associations between these survival classes and features of the abiotic and biotic environment in the plots. Unlike the results for germination rate, no significant associations were detected between survival rate and soil pH or bulk density (results not shown). However, seedling survival rate was significantly associated ($p = 0.0060$) with mean cover of leaf litter (average of May 2007 and June 2008 estimates): plots with a high percentage of seedlings surviving had significantly lower leaf litter cover (~ 64% leaf litter cover) than plots with no seedlings surviving to June 2008 (~ 80% leaf litter cover; Tukey-Kramer HSD comparison of means $p < 0.05$); plots with a low percentage of seedlings surviving had intermediate levels of leaf litter (~ 69%). No effect of herb layer cover (%) on seedling survival was apparent, but a significant positive association between species richness in plots and seedling survival rate was detected (Welch ANOVA $p = 0.0319$). Specifically, plots with high seedling survival had higher species richness than plots with zero survival (mean of 3.9 vs. 2.7 species per 0.25 m^2, respectively); plots with low seedling survival had intermediate species richness (3.4 species per 0.25 m^2).

Considering only plots beyond the range edge, a significant positive association was evident between seedling survival and soil pH (one-way ANOVA f ratio $p = 0.0328$). Plots with high survival had significantly higher pH than plots with zero survival (mean pH 6.3 vs. 5.8, respectively; Tukey-Kramer HSD pairwise comparison $p < 0.05$); plots with low survival had intermediate pH (mean pH: 5.9). A trend toward higher survival in plots with lower leaf litter cover was also evident, but not significant ($p > 0.10$). There was no evidence of an effect of soil bulk density, species richness, or herbaceous layer cover on seedling survival in plots beyond the range edge.

Associations between seedling growth rate and aspects of the abiotic and biotic environment were tested in the subset of plots with one or more seedlings surviving to June 2008 (i.e., 49 of the 79 plots, including plots both within and beyond range edge). Of the abiotic and biotic factors tested, only two showed marginally significant correlations with growth rate: species richness and soil bulk density. There was a positive correlation between species richness of plots and the mean total leaf area of seedlings in the plot ($R^2 = 0.06$, $p = 0.0995$). Similarly, a marginally significant trend toward higher growth rate in plots with lower soil bulk density was apparent ($R^2 = 0.06$, $p = 0.1034$). No effects of leaf litter cover (%), herb layer cover (%), or soil pH on growth rate were detected ($p >> 0.10$; results not shown).

Relationships between seedling growth rate and environmental factors were also tested for the subset of plots beyond the range edge with one or more seedlings surviving to June 2008. No significant or marginally significant correlations were apparent between growth rate in these plots and the abiotic and biotic factors tested (e.g., soil pH, herb layer cover; results not shown).

Discussion

The results of this study provide strong empirical evidence that the local distribution and geographic range of *J. diphylla* may be significantly limited by seed dispersal. In particular, the results of our descriptive survey show that the natural distribution of *J. diphylla* seedlings and juveniles is tightly clustered around adult plants, but experimental seed sowing at local and regional scales demonstrates the existence of suitable unoccupied habitat for seedling recruitment and growth both at local scales and beyond the species' range edge. To our knowledge, this is one of the few studies to have integrated experimental investigation of dispersal limitation at very local scales (e.g., meters to 10s of meters) and at large geographic scales (10s to 100s of km; but also see Van der Veken et al. 2007b). As such, the study's results provide some of the first empirical evidence for the type of non-equilibrial range dynamics inferred for dispersal-limited forest plant species by recent macro-ecological and bioclimatic niche modeling studies (e.g., Skov & Svenning 2004; Svenning & Skov 2007; Van der Veken et al. 2007a; Svenning et al. 2008).

Local Dispersal Limitation and Population Margins

Numerous studies have documented evidence for the dispersal limitation of forest plant species at local- to landscape-scales (e.g., Peterken & Game 1984; Matlack 1994; Brunet & Von Oheimb 1998; Bellemare et al. 2002). For example, ant-dispersed plant species and those with no obvious adaptations for seed dispersal tend to be absent from newly formed habitat patches (e.g., post-agricultural forests; Matlack 1994; Bellemare et al. 2002). Thus, the finding that *J. diphylla*, an ant-dispersed forest plant species, may be dispersal-limited at local scales is not surprising. Nevertheless, our results suggest that the spatial scale over which this phenomenon occurs is striking: Across 14 populations, the mean distance of seedlings to adult plants was ~ 0.3 m, with juveniles and ~ 95% of the 235 seedlings and juveniles observed were located < 1 m from adult plants. These data exhibited a form that was well-described by a log-normal distribution, a pattern that has been found to be typical of seed dispersal kernels for a number of non-wind-dispersed plant species (Figure 2.2; Harper 1977). Even outliers from this distributional pattern were not particularly distant: the furthest seedling was at 1.65 m and the furthest juvenile at 2.4 m from adult plants, though sampling extended to ~ 10 m. These findings fall near the lower end of observed dispersal distances and colonization rates for forest plant species (Matlack 1994; Brunet & Von Oheimb 1998; Cain et al. 1998; Gomez & Espadaler 1998; Van der Veken et al. 2007b). Overall, the results of the seedling and juvenile plant survey imply a relatively limited effectiveness or frequency of ant dispersal in *J. diphylla*. Most seedlings were located in positions that do not appear to necessitate explanation by any dispersal mechanism other than gravity, as the mean distance of seedlings and juveniles to adult plants (~ 33 and 23 cm, respectively) was similar to the average length of inflorescence stalks (~ 31 cm), many of which tilt toward the ground and release seeds at the margin of the plant's canopy when ripe (J. Bellemare, *personal observation*). Nevertheless, it is notable that several of the seedlings found at relatively 'extreme' distances from adult plants (~ 160-165 cm) were rooted in the remains of an abandoned ant nest in rotted wood (J. Bellemare, *personal observation*).

Although the tight clustering of seedlings and juveniles around adult *J. diphylla* plants could be the result of uniquely favorable micro-environmental conditions around adult plants, the results of our local seed sowing experiment along transects leading away from adult plants appear to discount this possibility. Even though some experimental plots yielded no seedlings, indicating that sites unsuitable for seed germination do exist, there were no clear meso-scale patterns to the distribution of suitable and unsuitable microsites along seed sowing transects running 40-50 m into unoccupied habitat. Germination rates did not decline substantially or systematically along most transects, even though naturally occurring seedlings were entirely absent from areas beyond ~ 1 m from adult plants in these populations. Of particular note, large numbers of seedlings appeared in plots at distances up to and beyond 100x the mean distance of naturally occurring seedlings from adult plants (i.e., 0.33 m vs. 30-50 m). These findings demonstrate that suitable unoccupied habitat for seedlings exists along and beyond the margins of natural *J. diphylla* populations and that the absence of seedlings in these areas is best explained by severe local seed dispersal limitation. Taken as a whole, the results of our local seed dispersal experiment may help to explain the tendency of *J. diphylla* to occur in dense populations with well-defined margins, surrounded by large areas of unoccupied habitat (Bellemare 2009a).

Suitable Sites Beyond Range Edges

Moving from evidence of local dispersal limitation to large-scale range dynamics, it is likely, *a priori*, that the northeastern range edge of *J. diphylla* may also be limited by seed dispersal, rather than abiotic or biotic factors (Bellemare 2009a). *Jeffersonia diphylla* populations near the species' northeastern range margin are of comparable size to, or larger than, range center populations, and the individuals comprising these range edge populations are significantly larger and more productive than range center individuals (Bellemare 2009a). These patterns of range-center to range-edge variation are inconsistent with geographic range models premised on species' distributional equilibrium with the environment, whereby population size and individual performance would be predicted to decline toward range margins (Brown 1984; Bellemare 2009a). Nevertheless, an abrupt range margin of the form seen at the northeastern range edge of *J. diphylla* could also potentially be explained by a substantial, step-like change in a single, limiting factor, rather than a gradual decline in suitability along multiple environmental gradients (Brown 1984; Hoffman & Blows 1994; Gaston 2003).

Given the close association of *J. diphylla* with calcareous soils and carbonate-rich bedrock (e.g., limestone; Gleason & Cronquist 1991; Bellemare 2009a), an abrupt or step-like change in bedrock geology would be a conspicuous environmental factor that could explain the species' unusual range edge in the Northeast. However, geologic maps for the region show that calcareous or carbonate-rich bedrock types (e.g., limestone, dolomite, calcareous shale, calcitic marble) are present in many areas to the east and north of the current range edge of *J. diphylla* (Zen 1983; Anonymous 1990; Anonymous 1997; Anonymous 1999; Anonymous 2000; Isachsen et al. 2000; Thompson & Sorenson 2000; Marvinney 2002; Figure 2.1). Indeed, the Hamilton Group and Onondaga Formation bedrock on which several large *J. diphylla* populations are located in western and central New York extends in a continuous belt to the east into the Hudson River Valley in eastern New York, even though no substantial populations of *J. diphylla* occur east of central New York (Figure 2.1; Isachsen et al. 2000). Likewise, large areas with limestone or marble bedrock elements are found in Vermont and western Massachusetts, and these regions include forested sites supporting a number of 'calciphile' plant species that co-occur with *J. diphylla* within its range (Bellemare et al. 2005; J. Bellemare, *personal observation*).

Taken together, the evidence of geologically suitable habitat beyond the species' current range margin and the presence of vigorous *J. diphylla* population's at the species' current range edge suggest that dispersal-limitation, rather than environmental limitation, is a plausible explanation for the current position of the species' range edge in the Northeast (Bellemare 2009a). The results of our experimental seed sowing beyond the species' range edge provide strong support for this hypothesis. Through relatively close matching of environmental conditions between within-range control sites and beyond-range treatment sites (Table 2.1), we found clear evidence for the existence of suitable, but unoccupied, habitat patches beyond the current range edge of *J. diphylla* in the Northeast. After two growing seasons, seeds planted beyond the range edge had established as young plants at a comparable rate to seeds planted within the range (~ 11% vs. 9%; Table 2.2), and these beyond-range plants were growing vigorously, with no signs of limitation by the abiotic or biotic environment (Table 2.2).

Rather than large-scale regional differences, similar micro-environmental factors seemed to drive *J. diphylla* seed germination and seedling survival dynamics at both within- and beyond-range sites. For example, across plots in both regions, seed germination rates showed a significant quadratic relationship with soil pH, with germination peaking around pH 6 (Figure 2.5). This pattern is suggestive of an edaphic niche for optimal seed germination, and is consistent with prior evidence of the species' preference for soils with circumneutral pH (Bellemare 2009a). Similarly, a quadratic relationship with soil bulk density was also detected, with the highest germination observed at moderate bulk density (Figure 2.4); this pattern is suggestive of another important axis in the species' seedling or regeneration niche (cf. Grubb 1977).

Beyond soil chemistry, seedling establishment and survival to the second growing season showed a negative association with the cover of leaf litter in experimental plots within and beyond the species' range edge. Seedlings in plots with thick leaf litter often died after being buried as leaves accumulated or shifted in the plot. In contrast, seedling survival and establishment were significantly higher in areas where less leaf litter accumulated, such as on slopes or convex areas.

Interestingly, the recruitment or regeneration niche of *J. diphylla* inferred from these data (i.e., circumneutral pH, loose soil, low leaf litter cover) also appears to be well-suited for other forest plant species: rather than showing a negative relationship with species richness or herb layer cover, *J. diphylla* seedling germination and establishment were found to be positively correlated or associated with these aspects of the biotic community. This pattern may suggest a limited role for certain biotic factors (e.g., plant x plant competition) in determining the outcome of seed germination and establishment dynamics.

While the existence of suitable but unoccupied habitat within range limits has been demonstrated for a number of plant species (e.g., Primack & Miao 1992; Ehrlen & Eriksson 2000; Moore & Elmendorf 2006), fewer studies have found evidence for the existence of such sites beyond range edges (see recent review in Gaston 2009; also: Holland 1980; Van der Veken et al. 2007b). However, of particular note in regards to the present study is the degree to which several metrics of plant performance *increased* at sites beyond the range edge. Germination rates were over 2x higher at sites beyond the range edge than at occupied sites within the range (~ 48% vs. ~ 21%, $p < 0.0001$; Table 2.2). Similarly, seedling and juvenile growth rates, as measured by leaf size and total leaf area in the second growing season, were also significantly higher outside the range (Table 2.2). Equally striking was the higher rate at which seedlings beyond the range edge transitioned to the two-leaved juvenile life stage in their second growing season when compared to plants at control sites (~ 16% vs. 3%, beyond- vs. within-range, respectively). This suggests that the experimental sites beyond the range margin may include highly suitable habitat for *J. diphylla* recruitment and growth.

Some aspects of the increased performance of *J. diphylla* plants beyond the species' range margin appear to be linked to environmental differences between within- and beyond-range sites. While key aspects of soil chemistry were comparable between the two areas (e.g., in terms of soil pH and calcium content), physical properties of the soils differed substantially: beyond-range sites had soils composed of substantially more sand than within-range soils (76% vs. 39%, respectively) and, in parallel, clay was almost absent from soils at the beyond-range sites, while it comprised a substantial component of within-range soils (< 1% vs. 13%, respectively; Table 2.1). This difference in soil texture is noteworthy, as prior work has found increased performance of *J. diphylla* populations on soils with higher sand content within its natural range (Bellemare 2009a); however, the sand content of soils at the beyond-range sites falls outside the range of natural variation in sand content observed at within-range sites. That the species' performance might increase on soil types it does not encounter within its natural range might be cautiously predicted from the descriptive data presented in Bellemare (2009a), but the experimental evidence that this might actually be the case seems remarkable.

The other edaphic factor that varied between regions in a manner consistent with the increased performance of *J. diphylla* beyond its range edge was soil bulk density. Seed germination rates showed a significant quadratic correlation with soil bulk density, with the highest germination rates observed at moderate bulk densities (Figure 2.4). A significant difference in soil bulk density between the two regions ($p < 0.0001$; Table 2.1), with beyond range sites having looser, lower bulk density soils, resulted in a greater proportion of beyond-range plots having bulk densities near the apparent peak in suitability for seed germination.

Both edaphic factors associated with plant performance (i.e., soil sand content and bulk density) are likely linked to regional patterns of soil formation, surficial geology, and bedrock geology. While both within- and beyond-range sites are situated north of the Pleistocene glacial boundary, the composition of the glacial deposits forming the parent material for these soils differs. The within-range sites lie in a region underlain almost exclusively by fine-textured, sedimentary bedrocks (Isachsen et al. 2000); the glacial till and soils derived from these rocks tend to be fine-textured, with substantial silt and clay content (Bellemare 2009a). In addition, fine-textured peri-glacial lake deposits near some of the within-range sites may further contribute to the increased silt and clay content of the soils at these sites (Caldwell et al. 1986); these fine particles appear to contribute to higher soil bulk densities. At the beyond-range sites, soils have developed almost exclusively in glacial till derived from the crystalline metamorphic and igneous bedrocks of western New England; unlike within-range bedrocks, this parent material contains a substantial quantity of quartz and other weathering-resistant, sand-forming minerals (Segerstrom 1955; Brady 1990; Bailey 2000). In addition, the calcitic marble bedrock responsible for the calcareous conditions at the beyond-range sites contains up to 50% clastic quartz, which, with weathering, likely contributes further to the sand content of the soils (Segerstrom 1956). As such, areas beyond the current range edge appear to provide a combination of edaphic conditions (i.e., coarse-textured, low bulk density, calcareous soils) that are not found within the species' natural range, but that are nonetheless highly suitable for seedling and juvenile growth (Bellemare 2009a).

In a broader context, these findings also appear to highlight the potential for unpredictable or non-linear population dynamics in species shifting their distributions in response to climate change. Specifically, even as species' geographic ranges may shift in order to track suitable climatic conditions (e.g., temperature, rainfall), the underlying geologic and edaphic 'template' of the landscape will remain largely static. This implies that species may encounter novel geologic or edaphic conditions as their distributions shift across the landscape, even if they manage to remain within similar climatic envelopes through dispersal and habitat tracking. For plants, novel geologic or edaphic conditions may trigger unpredictable changes in key demographic parameters, such as germination rates, establishment, or growth rates due to the fundamental role that soil conditions may play in these processes. Our results demonstrating increased performance of young *J. diphylla* growing beyond the species' range edge on the 'novel' conditions of coarse-textured, calcareous soils may provide an example of such a phenomenon. This pattern may also be indicative of the species' fundamental or potential niche including environmental space that the species does not currently encounter within its native range, a dynamic that may be relatively common during episodes of rapid climate change (Jackson & Overpeck 2000; Ackerly 2003).

Reconciling Long-Distance Dispersal and Dispersal-Limited Range Edges

When seeds of *J. diphylla* were experimentally sown in areas ~ 300 km beyond the species' current range edge, vigorous seedlings and juveniles resulted (Table 2.2; Figure 2.1). This finding suggests that if naturally-dispersed seeds were reaching these sites, *J. diphylla* would be present, at least as seedlings or juvenile plants. However, natural occurrences or populations of the species have never been documented in the region (Gleason & Cronquist 1991; Sorrie & Somers 1999; Magee & Ahles 2007). From this, we infer that the northeastern range limit of *J. diphylla* is limited by seed dispersal, not by contemporary environmental conditions. As such, the species appears to provide one of the few empirically-documented examples of a non-equilibrial range edge in a dispersal-limited plant species (Davis 1986; Holt et al. 2005; Van der Veken et al. 2007a, 2007b; Svenning et al. 2008; Gaston 2009). This finding also implies that the significant dispersal limitation documented for *J. diphylla* at local scales (e.g., Figures 2.2, 2.3) may also be evident at the scale of the species' geographic range, a conclusion that runs counter to predictions that local dispersal dynamics and large-scale range dynamics may be largely disconnected due to the key role of rare, non-standard dispersal events in processes like range expansion (e.g., Cain et al. 1998; Higgins et al. 2003a; Nathan 2006).

Even so, the relationship between local dispersal patterns and long-distance dispersal is not straightforward, as has been well-documented by previous researchers (e.g., Clark 1998; Cain et al. 1998; Higgins et al. 2003a; Nathan 2006). For example, in the case of *J. diphylla*, a potential post-glacial migration route for the species, following an arc of calcareous bedrock from the Pleistocene glacial margin in northeastern Ohio to the species' current range margin near Syracuse, New York, covers approximately 550 km. Given that recent phylogeographic studies indicate that some temperate forest plant species may have persisted up to within 500 km of the Laurentide Ice Sheet (e.g., McLachlan et al. 2005), this suggests that *J. diphylla* would have to have migrated, at minimum, ~ 1000 km during the post-glacial, Holocene epoch (last ~ 11-12 ky) to reach its current range boundaries in the Northeast. This results in an estimated migration rate of close to ~ 100 m per year on average. The results of our study make clear that dispersal and colonization distances of this magnitude are unlikely in present-day populations, where the vast majority of seedlings are located < 1 m from adult plants (Figure 2.2). This striking discrepancy between inferred migration rates and field-based measures of dispersal patterns reaffirms the conclusions of earlier researchers that rare, long-distance dispersal events must have played a pivotal role in the post-glacial migration and range expansion of temperate forest plants that occupy formerly glaciated regions (Clark 1998; Cain et al. 1998). The nature of such rare long-distance dispersal events is largely a matter of speculation, but occasional ingestion and movement of seed between habitat patches by white-tailed deer (*Oidocoileus virginianus*) is a possibility, given observations of this 'non-standard' dispersal mode in another ant-dispersed forest herb in the region (i.e., *Trillium grandiflorum*; Vellend et al. 2003).

Despite the inference that long-distance dispersal events have been involved in the Holocene range expansion of *J. diphylla*, the results of this study provide compelling evidence that the species' range expansion into the Northeast may still be incomplete due to seed dispersal limitation. Reconciling these two points may require recognizing that, while undoubtedly crucial to explaining many plant species' current distributions, long-distance dispersal may not universally overcome dispersal-related limitations to range expansion in all species. The potential and scale of rare long-distance dispersal events may vary substantially among plant species, leading some to rapidly obtain distributions in 'dynamic equilibrium' with changing environmental conditions, while the distributions of other species may lag considerably behind such environmental changes (Davis 1986; Webb 1986). While the role of plant life history traits (e.g., seed dispersal mode, seed number) in determining species potential for long-distance dispersal has been questioned (e.g., Cain et al. 1998; Clark 1998), the dispersal-related life history traits of *J. diphylla* seem a likely driver of its dispersal limitation. More broadly, as proposed by Van der Veken et al. (2007a), it may be the case that plant species with differing 'standard' dispersal modes may also have differing propensities for 'non-standard' long-distance dispersal, due to differences in the dispersal-related morphology of propagules (e.g., plumed vs. unplumed), seed production levels (e.g., 10s vs 1000s of propagules; Mabry 2004), or other plant traits correlated with reproduction and phenology (e.g., inflorescence height, spring vs. summer fruit ripening; Thompson 1981). As such, a short-statured forest herb like *J. diphylla* that produces 10s of ant-dispersed seeds per year will have fewer opportunities for its seeds to be caught up in the types of rare events that occasionally move seeds long distances (e.g., windstorms, ingestion by vertebrates, adhesion to vertebrates).

Despite the general sense that the key role of 'non-standard' long-distance dispersal events in range expansion largely negates the relevance of life history traits and observations on 'standard' dispersal (e.g., Cain et al. 1998; Clark 1998), researchers investigating long-distance dispersal are increasingly focusing on small-scale dynamics at the initiation of dispersal to understand the factors controlling the probability of such rare events (Bohrer et al. 2008; Bullock & Nathan 2008; Soons & Bullock 2008). As these studies have demonstrated that minor variations in the timing of seed release or vegetation structure can have significant impacts on the potential for long-distance dispersal (e.g., Bohrer et al. 2008; Soons & Bullock 2008), the proposition that species with qualitatively different seed morphology and associated plant structure might have differing propensities for long-distance dispersal and migration appears reasonable. Indeed, comparative data showing differences in range size among species with differing seed dispersal modes indicates that such an effect is probable, particularly in areas with a history of 'recent' recolonization (e.g., regions impacted by Pleistocene glaciation and climate change; Van der Veken et al. 2007a).

Conclusions

Because *J. diphylla* is a slow-growing, long-lived perennial and the experimental components of this study covered only three years and two growing seasons, there are inevitable caveats to the scope of our conclusions. As true colonization requires full plant maturation and successful reproduction, it will be necessary to follow the experimental plants described in this study for additional growing seasons in order to document whether they eventually flower and produce viable seeds beyond the species' range margin. Further, it is also possible that rare events (e.g., extreme winter cold or insect outbreaks), rather than average environmental conditions, may determine the species' distributional limit in the study area (Gaston 2003). In both cases, these possibilities are difficult or impossible to evaluate over the course of a single 2-3 year field study. Nonetheless, some insight to these points is available from the longer-running, 'accidental experiment' of horticulture, where native plants are frequently grown beyond their range edges. In semi-natural garden settings beyond its range edge in the Northeast, *J. diphylla* is a long-lived perennial and regularly produces viable seeds and seedlings (Cullina 2000; J. Bellemare, *personal observation*). While it is still conceivable that the species' distribution is limited by extreme events with a return interval of many decades to centuries, rather than dispersal limitation, this possibility would appear to imply that seedlings, juveniles, and adult plants should occasionally appear beyond the current range edge; however, this is generally not the case and *J. diphylla* has never been documented in western New England where our beyond-range plots were located (Sorrie & Somers 1999; Magee & Ahles 2007).

In conclusion, substantial descriptive, circumstantial, and experimental evidence indicates that the northeastern range edge of *J. diphylla* is not in equilibrium with the contemporary environment (Bellemare 2009a; this study). The geographic scale of this phenomenon and the apparent stasis of the species' range edge on historical timescales suggests that the current range margin may represent a slow-moving colonization 'wavefront' moving into the region from areas to the south and west (Holt et al. 2005; Bellemare 2009a). The average colonization distance observed for natural seedlings in the field (~ 33 cm) and the distance from non-glaciated regions to the species' current range edge in the formerly-glaciated Northeast (~ 1000 km) suggests that it is entirely possible that such a colonization front may trace to long-term time lags in post-glacial range expansion; indeed some level of rare long-distance dispersal is required to even explain the species' ability to reach its current range margin in central New York (cf. Cain et al. 1998). The possibility of non-equilibrial range edges has been described in theoretical considerations of range margins (e.g., Holt et al. 2005; Gaston 2009), and their existence has been inferred from macro-ecological studies (e.g., Van der Veken et al. 2007a; Svenning et al. 2008), but few studies have provided clear field-based, empirical evidence of such a phenomenon. While most models of geographic ranges and range edges are premised on species' distributional equilibrium with the environment, the results of this study make clear that long-term, large-scale 'disequilibrium' is possible for some species (Davis 1986). Indeed, in that *J. diphylla* is not atypical of many forest plants, the potential for this phenomenon among other plant species is clear (e.g., Van der Veken et al. 2007a). As the effects of anthropogenic climate change increase in the future, the possibility that some dispersal-limited species will be unable to rapidly track changing conditions will need to be incorporated into conservation strategies (Bellemare 2009b).

APPENDIX

Locations of 14 *Jeffersonia diphylla* populations surveyed for the distribution of seedlings and juveniles relative to adult plants in June 2008. Quadrats measured 0.5 x 0.5 m in size.

Site Name	**Location**	**Quadrats sampled**
Hardy Creek	Trimble Co., KY	22
Raven Run	Fayette Co., KY	30
Salt-Peter Cave	Casey Co., KY	28
Sexton Creek	Clay Co., KY	25
Clifty Falls	Jefferson Co., IN	20
Monroe Lake	Monroe Co., IN	43
Fox Lake	Athens Co., OH	25
Stroud’s Run	Athens Co., OH	31
Great Gully	Cayuga Co., NY	23
Keshequa Creek	Livingston Co., NY	22
Martisco Woods	Onondaga Co., NY	26
Railroad Mills	Ontario Co., NY	25
Two Mile Creek	Livingston Co., NY	25
Venice Woods	Cayuga Co., NY	22

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CHAPTER 3

THE PROSPECTS FOR ‘ASSISTED COLONIZATION’ IN THE TEMPERATE DECIDUOUS FOREST BIOME: WILL ENDEMIC PLANT SPECIES REQUIRE HUMAN INTERVENTION TO SURVIVE CLIMATE CHANGE?

Abstract

‘Assisted Colonization’ is a new and controversial conservation strategy that aims to save species from anthropogenic climate change by intentionally translocating them to areas where they have not occurred historically, but where they are expected to survive as climate changes. This unconventional strategy has already generated vigorous debate and discussion among scientists and policy makers. Major questions remain as to the necessity, feasibility, and risk of assisted colonization, as well as to the scope and types of species that might require such direct intervention. Beyond broad statements on the general characteristics of species that may benefit from assisted colonization (e.g., less vagile species), no studies have provided a biome-level assessment of the types or groups of species, among the many thousands comprising most biomes, that might require assisted colonization to avoid extinction. Here we review a range of ecological, paleoecological, biogeographical, and evolutionary sources to provide a biome-level assessment of the prospects for assisted colonization as a conservation strategy for plant species of the Temperate Deciduous Forests of eastern North America and Europe. Among the many plant species comprising this biome, a range of evidence suggests that range-restricted ‘paleoendemics’ represent a group with high vulnerability to rapid climate change, reasonable probability of successful large-scale translocation, limited ecological risk, and significant value for biodiversity conservation. The study also highlights key areas in need of further

research to better elucidate the viability of assisted colonization as workable conservation strategy in the 21st century.

Introduction

Climate change in the 21st century is expected to cause the redistribution of species in many regions of the globe and has been projected to result in high rates of extinction (Parmesan & Yohe 2003; Thomas et al. 2004; Hickling et al. 2006; Schwartz et al. 2006; Hoegh-Guldberg et al. 2008). The bulk of these extinctions are likely to occur when species are unable to track changes in the geographic distribution of their favored climatic niche, either due to inherently slow rates of dispersal or because of habitat fragmentation and barriers to migration caused by human modification of the landscape (e.g., agricultural land use, urban development; Thomas et al. 2004; Hoegh-Guldberg et al. 2008). The prospect of extinctions due to dispersal limitation has led some researchers to suggest that direct human intervention may be necessary to assist species in colonizing new areas of suitable habitat beyond their current range boundaries (McLachlan et al. 2007). Variously termed 'assisted migration', 'managed relocation', or 'assisted colonization', this new and largely unprecedented conservation strategy has already generated substantial interest and controversy among biologists and conservationists (Barlow & Martin 2004; Schwartz 2004; McLachlan et al. 2007; Hoegh-Guldberg et al. 2008; Ricciardi & Simberloff 2009; Richardson et al. 2009).

While some discussion of conservation strategies involving large-scale species translocations to areas outside their native range dates to the early 1990s (e.g., Davis & Zabinski 1992; Peters 1992), recent interest in the subject was largely triggered by the activities of a private group, Torreya Guardians, whose goal is to expand the geographic distribution of the Florida panhandle endemic *Torreya taxifolia* (a coniferous tree species) northward into the Appalachian Mountains of eastern North America (Barlow & Martin 2004; Schwartz 2004; McLachlan et al. 2007). Subsequent to this narrowly-focused debate, biologists have begun to address the broader conceptual and legal issues framing such intentional species translocations, and to provide general overviews of the characteristics of species threatened by anthropogenic climate change that might benefit from assisted colonization (McLachlan et al. 2007; Hunter 2007; Hoegh-Guldberg et al. 2008). Concurrently, other researchers have focused in greater detail on the invasive potential and ecological risks associated with translocating species beyond their native ranges (Schwartz 2004; Mueller & Hellman 2008; Ricciardi & Simberloff 2009), as well as presenting frameworks for incorporating socioeconomic considerations into the evaluations of assisted colonization proposals (Hoegh-Guldberg et al. 2008; Richardson et al. 2009).

However, beyond preliminary suggestions that assisted colonization would be best implemented within ‘broad biogeographic region[s]’ and for species with ‘limited vagility’ (Hunter 2007; Hoegh-Guldberg 2007), few studies have grappled directly with the daunting prospect of identifying candidate species for assisted colonization from among the many thousands comprising most biomes. While limited vagility is an intuitively obvious characteristic that might be used to identify species of concern (Hunter 2007), little is known about the actual dispersal capabilities of most species and many life history traits suggestive of restricted dispersal ability are present in species that have nonetheless migrated long distances in response to past climate change (Cain et al. 1998; Clark 1998). While acquiring more direct empirical estimates of species’ dispersal capabilities would be ideal for evaluating potential target species and the spatial scale over which assisted colonization efforts might be implemented, substantial time and research effort are required to investigate dispersal patterns even for a single species (e.g., Bellemare 2009). Furthermore, the types of dispersal most likely to contribute to large-scale migration and poleward range shifts (i.e., rare long distance dispersal events) typically elude direct empirical investigation and are often inferred *post hoc* (e.g., Cain et al. 1998), making the prediction of future migration potential prone to substantial uncertainty (Higgins et al. 2003; McLachlan et al. 2007). Given these challenges, it is apparent that other, indirect, approaches to evaluating large groups of species for vulnerability to climate change are needed. Moreover, because assisted colonization presently exists chiefly as a hypothetical, with little data to evaluate its actual feasibility or risk (but see: Willis et al. 2009; Pelini et al. 2009), it is crucial that candidate species be identified early in order to facilitate the types of exploratory empirical research that will be necessary to determine whether assisted colonization is a viable conservation option.

To that end, this review synthesizes information from a range of ecological, paleoecological, biogeographical, and evolutionary sources to provide a preliminary evaluation of the prospects and feasibility of assisted colonization for plant species of the Temperate Deciduous Forest biome. Specifically, we evaluate the impacts of past climate change on this biome and ask whether the biogeographical patterns produced by these historical dynamics may offer insight to the types of plant species most vulnerable to future threats. Such an approach is increasingly recognized as key to developing realistic biome-wide assessments of the risks posed by future climate change (Petit et al. 2008; Cannon et al. 2009). We address four key concerns: 1) What types or emergent groups of plant species are most likely to be vulnerable to the impacts of anthropogenic climate change? 2) To what extent might assisted colonization be a necessary step to avoid extinctions among these species, as opposed to other, less intrusive, approaches, such as increasing landscape connectivity? 3) Do different types of candidate species differ in their likelihood of successful establishment following large-scale translocation, and are such large-scale translocations feasible even under current climatic conditions? 4) What might be the relative ecological risks associated with assisted colonization of different types of candidate species? We believe that such a synthetic biome-wide approach, grounded in regional biogeographic and evolutionary history, may serve as a model for the types of evaluations that will need to be undertaken in other bioregions to evaluate the need, feasibility, and risks of assisted colonization.

Temperate Deciduous Forests: Origin and History Relative to Climate Change

Temperate Deciduous Forests (TDF) are found primarily in the Northern Hemisphere in areas where moderate moisture and temperature levels during the summer, followed by cold or sub-freezing temperatures in winter, promote the dominance of large-statured trees with winter-deciduous leaves (Walter 1973; Ellenberg 1988; Greller 1988; Gurevitch et al. 2002). This biome traces its origin to the late Cretaceous period (~ 100-65 million years ago, mya) when several key angiosperm forest tree lineages, including Aceraceae, Fagaceae, and Juglandaceae first appeared and rose to prominence (Manchester 1999; Willis & McElwain 2002; Wang et al. 2009). During the Tertiary (~ 65-1.8 mya), relatively warm and wet climatic conditions, combined with greater connectivity in the Northern Hemisphere, allowed TDF to extend across large portions of North America and Eurasia, including many northern areas now occupied by boreal forest, tundra, or arctic desert (Manchester 1999; Qian & Rickleffs 1999; Wen 1999; Tiffney & Manchester 2001; Willis & McElwain 2002). With the onset of climatic cooling and drying in the late Tertiary, and the advent of extensive continental glaciations in the Quaternary period (~ 1.8 mya to present), the geographic distributions of TDF plant species were forced south and fragmented through a series of dramatic climate-driven range contractions (Davis 1983; Latham & Ricklefs 1993;

Delcourt 2002). Presently, TDF persists in several widely disjunct regions in the Northern Hemisphere, with prominent examples in eastern North America, Europe, and eastern Asia (Ricklefs & Latham 1993; Manchester 1999; Wen 1999).

Past climate change has been linked to the extinction or regional extirpation of numerous TDF plant species (Davis 1983; Latham & Ricklefs 1993; Svenning 2003). In particular, the climatic deterioration of the late Tertiary and Quaternary led to the regional extinction of large numbers of TDF plant lineages in Europe, including *Carya*, *Hamamelis*, *Liriodendron*, *Magnolia*, *Tsuga*, and upwards of 80 other woody plant genera (Davis 1983; Latham & Ricklefs 1993; Svenning 2003). Fewer extinctions are documented for eastern North America, but this period did see the extirpation of at least 8 woody plant genera in the region, including *Dendropanax*, *Platycarya*, *Pterocarya*, and *Sciadopitys* (Latham & Ricklefs 1993; Willard 1994; Manchester 1999; Tiffney & Manchester 2001). In contrast, representatives of many of the lineages extirpated in Europe and eastern North America persist to this day in the TDF of eastern Asia, where species losses appear to have been buffered by the region's greater topographic heterogeneity and lack of extensive continental glaciation (Huntley 1993; Latham & Ricklefs 1993; Qian & Ricklefs 1999). Notably, the large number of late-Tertiary and early Quaternary plant extinctions in Europe have resulted in the striking differences in contemporary species diversity seen when contrasting European TDF with similar forests in eastern North America or eastern Asia (Davis 1983; Huntley 1993; Latham & Ricklefs 1993; Svenning 2003). These biogeographical patterns underscore the potential for severe and long-lasting impacts of modern, anthropogenic climate change on the TDF biome (Delcourt 2002; Petit et al. 2008).

In the 21st century, plant and animal species are confronted with a new climatic challenge of similar magnitude to the dramatic climate changes of the late Tertiary and

Quaternary: anthropogenic climate change or ‘global warming’ (Delcourt 2002; Parmesan et al. 2003; Thomas et al. 2004). Anthropogenic climate change is predicted to cause the wholesale redistribution of plant and animal species on a scale not seen since the end of the Pleistocene and, given its unprecedented rate, may endanger the biological diversity of many biomes (Iverson & Prasad 1998; Delcourt 2002; Thomas et al. 2004; Schwartz et al. 2006). In both eastern North America and Europe, TDF are projected to be substantially impacted by these changes, with the distribution of climatically-suitable habitat for many forest plant species shifting northward or to higher elevation, potentially resulting in population declines or regional extinction across large areas of the present TDF biome (Iverson & Prasad 1998; Honnay et al. 2002; Skov & Svenning 2004; Schwartz et al. 2006; Sveening & Skov 2006; Morin et al. 2008).

What Types of TDF Species May Be Most Vulnerable to Climate Change?

It is clear from past episodes of climate change and future climatic projections that not all species are equally threatened by changing climate (Svenning 2003; Thomas et al. 2004; Thuiller et al. 2005a; Schwartz et al. 2006; Willis et al. 2007). For example, the ongoing poleward range shifts of many bird, mammal, and insect taxa suggest that some relatively vagile species may already be adjusting their distributions in response to anthropogenic climate change (Parmesan & Yohe 2003; Hickling et al. 2005; Zuckerberg et al. 2009). Similarly, paleoecological evidence from past episodes of climatic change indicates that many plant species may also be capable of relatively rapid range adjustments (Clark 1998). Nevertheless, the substantial numbers of regional extirpations and extinctions associated with past episodes of climate change suggest that not all species are equally resilient to such climatic dynamics (Latham & Ricklefs 1993; Svenning 2003; Willis et al. 2007).

Of greatest concern in the face of anthropogenic climate change are species with limited geographic distributions, such as narrow endemics (Thomas et al. 2004; Parmesan 2006; Schwartz et al. 2006). The increased extinction risk of small-ranged species traces to the substantial disjunctions projected between the locations of these species' current ranges and the distribution of climatically-similar areas in the future (Thomas et al. 2004; Schwartz et al. 2006). Such disjunctions between present and future habitat areas are less likely for widespread species, where some portions of broadly-distributed species' ranges are likely to remain suitable into the future, even as other areas may deteriorate (Thomas et al. 2004; Schwartz et al. 2006).

Given the disjunctions between present and future potential habitat for small-ranged species, many narrow endemics may need to accomplish substantial long-distance dispersal and colonization of areas beyond their current range limits in order to survive rapid climate change (Thomas et al. 2004; McLachlan et al. 2007). However, for some small-ranged species, limited geographic distributions may be the outcome of these species' very inability to successfully disperse and expand their ranges on time scales relevant to anthropogenic climate change (Oakwood et al. 1993; Lloyd et al. 2003; Van der Veken et al. 2007a; Rossetto et al. 2008). Complicating matters further, significant questions remain on the relative importance of climate in limiting the distributions of small-ranged endemic species; specifically, it is likely that some types endemics are limited by factors other than climate, such as soil conditions, and might be relatively resilient to moderate levels of climate change (Estill & Cruzan 2001; Schwartz et al. 2006; McLachlan et al. 2007). Overall, it is clear that evaluating endemic species' vulnerability to climate change, and devising appropriate conservation measures, will require moving beyond simple characterizations of distributional patterns (i.e., small range size) to gain further insight to the varying ecological, biogeographical, and evolutionary processes that can produce patterns of narrow endemism in plant species.

Ecologists have long recognized that the restricted distributions of endemic species may be the outcome of a variety of causes (Willis 1922, Wherry 1944, Stebbins and Major 1965, Daubenmire 1978). Among potential causes of endemism, the most commonly cited are species' innate biological or ecological characteristics (e.g., competitive inferiority or association with uncommon habitats; Daubenmire 1978, Baskin and Baskin 1989, Lavergne 2004), their recent evolutionary origin (Stebbins and Major 1965, Lesica et al. 2006), or endemism due to the fragmentation or marginalization of a formerly more extensive range (Daubenmire 1978). These three general classes of endemic species have been labeled 'ecological endemics', 'neoendemics', and 'paleoendemics', respectively (Stebbins and Major 1965; Daubenmire 1978; Estill & Cruzan 2001).

In addition to these traditional explanations for the small ranges of endemic species, recent research has also highlighted the possibility that dispersal limitation may play a pivotal role in determining the limited geographic distributions of some species (Kropf et al. 2002; Rossetto & Koyyman 2005; Svenning & Skov 2007a; Van der Veken et al. 2007a, 2007b; Rossetto 2008). In the case of ecological endemics that are associated with unusual habitats (e.g., serpentine bedrock), suitable habitat patches are often of limited spatial extent and widely scattered in a matrix of unsuitable habitat, likely making inter-site dispersal rare and range expansion improbable. For neoendemics, limited dispersal may be a contributing factor to small range size, as recently evolved species have had limited time to disperse and expand their ranges (Lesica et al. 2006). Dispersal limitation may also be a key factor controlling the distributions of some paleoendemics (Rossetto & Koyyman 2005; Rosetto 2008). While prior considerations of paleoendemics have frequently focused on the range fragmentation and decline leading to these species' restricted distributions (Daubenmire 1978), it is also apparent that their failure to expand their distributions subsequent to such historical events, when conditions have ameliorated, may be correlated with limited dispersal ability (Svenning & Skov 2007a; Van der Veken et al. 2007a). Overall, the prominent role that dispersal limitation may play in limiting the distributions of many endemic species suggests that these species will be limited in their ability to respond to anthropogenic climate change.

As in other plant species, dispersal limitation of endemics may trace to a range of biological traits or characteristics, as well as to aspects of the extent and spatial distribution of their preferred habitat. For example, ecological and macroecological studies have shown that factors such as low seed production, a lack of morphological adaptations for long distance seed dispersal, or the absence of suitable dispersal agents may lead to dispersal limitation in plants (Janzen and Martin 1982, Matlack 1994, Barlow 2000, Bellemare et al. 2002, Verheyen et al. 2003, Van der Veken et al. 2007a). Such characteristics may contribute to limited range expansion in some plant species (Oakwood et al. 1993; Barlow 2000; Lloyd et al. 2003; Van der Veken et al. 2007a). Aspects of landscape structure and the relative isolation of suitable habitat patches may lead to dispersal limitation and restricted range size of other endemics, even for those with moderate dispersal capabilities.

Further evidence for dispersal limitation in causing patterns of endemism is provided by 'hotspots' of endemism, where relatively large numbers of endemic species co-occur (Myers et al. 2000; Estill & Cruzan 2001; Jansson 2003; Finnie et al. 2007; Médail & Diadema 2009). Globally, such concentrations of endemic species are typically associated with areas that have experienced relatively stable climatic conditions over long periods of time (Jansson 2003). In the Northern Hemisphere, endemic hotspots often coincide with the locations of putative glacial 'refugia', where large numbers of TDF taxa persisted during the glacial maxima and climatic oscillations of the Pleistocene (Estill & Cruzan 2001; Jansson 2003; Svenning & Skov 2007a, 2007b; Médail & Diadema 2009). Notably, narrowly-distributed endemic species are largely absent from formerly glaciated regions and areas where climatic conditions were relatively extreme during the Quaternary (Stein et al. 2000; Jansson 2003; White et al. 2003; Finnie et al. 2007). While many TDF species have successfully expanded from such glacial refugia to recolonize northern areas during the post-glacial Holocene (Cain et al. 1998; Clark 1998; Delcourt 2002), the numerous paleoendemic plant species that are still restricted to such refugial areas, even after 10-11 ky of the present interglacial, suggests that dispersal limitation may be a significant and long-standing limit on range expansion in these species (Estill & Cruzan 2001; Svenning & Skov 2007a, 2007b; Van der Veken et al. 2007a).

While the co-occurrence of TDF endemics in hotspots might facilitate conservation planning under 'normal' conditions, the localization of these refugial areas to the southern margins, or to areas south of, the main TDF areas in eastern North America and Europe is troubling in the face of anthropogenic climate change (Estill & Cruzan 2001; Mejías et al. 2002, 2007; Hampe & Petit 2005; Médail & Diadema 2009). Indeed, in some cases the climatic conditions in these southern refugial areas may already be marginal for TDF endemics (e.g., Schwartz 2004; Mejías et al. 2002, 2007). Further, the isolation of many of these endemic hotspots in restricted areas with conditions that are cooler or more mesic than the surrounding landscape suggests that the potential for gradual, diffusive range expansion may be limited. For example, populations of the paleoendemic *Rhododendron ponticum* on the Iberian Peninsula are localized to cool, moist riverside sites, but even here the species exhibits severe recruitment limitation due to dry summer conditions (Mejías et al. 2002, 2007).

Overall, while researchers have repeatedly indicated that small range size and dispersal limitation might be predictors of species' vulnerability to climate change (Thomas et al. 2004; Schwartz et al. 2006; Hunter 2007; Hoegh-Guldberg et al. 2008), the possibility that these two species 'characteristics' might themselves be causally linked (e.g., Oakwood et al. 1993; Lloyd et al. 2003; Van der Veken et al. 2007a) has not been widely recognized or its implications for species conservation in the face of climate change considered. However, it has become increasingly clear that in regions substantially affected by past climate change, range size and relative restriction to past refugial areas may provide insight to species' long-term dispersal capabilities and potential vulnerability to future climate change (Svenning & Skov 2007a, 2007b; Van der Veken 2007a).

Will Vulnerable TDF Species Require Assisted Colonization to Avoid Extinction?

The possibility that dispersal limitation and small range size may be causally linked in some species has profound implications for conservation planning in the face of anthropogenic climate change (Van der Veken et al. 2007a). Additionally, in a more geographically explicit context, the localization of many endemic hotspots to the southern margins of the TDF biome, due to the impacts of past climatic *cooling* during the Quaternary, implies that the geographic ranges of many endemic species, as well as unique intra-specific variants of more widespread species, may be poorly positioned to withstand future climatic *warming* (Delcourt 2002; Hampe & Petit 2005; Wilson et al. 2005). While endemic hotspots are often associated with areas that have exhibited relative climatic stability in the past (e.g., not glaciated, not extremely cold or dry), many of these areas are still predicted to be substantially affected by future climate change (Jansson 2003). Notably, relict populations of a number of boreal and TDF species already exhibit limited or failing recruitment at their southern range edges in Europe (e.g., García et al. 1999; Hampe & Arroyo 2002; Mejías et al. 2002, 2007;

Castro et al. 2004), and populations of *Torreya taxifolia*, the catalyst for debate on assisted colonization in eastern North America, have declined precipitously in the wild during the 20th century, potentially linked to climate change or pathogen attack enhanced by climate change (Barlow & Martin 2004; Schwartz 2004).

Conservationists have frequently stressed the importance of increased landscape connectivity to facilitate species' natural dispersal and range shifts in response to anthropogenic climate change (Hunter et al. 1988, Hannah et al. 2002, Hunter 2007); however, this approach may prove ineffective for species that are severely dispersal-limited, or for those whose present ranges and potential future habitat are separated by large expanses of naturally unsuitable habitat. Indeed, the rate of anthropogenic climate change may even pose challenges for well-dispersed species, as some studies have projected that migration rates will need to approach 3000-5000 m/year in order to keep pace, but even the 'fastest' plant migrations of the late Pleistocene and Holocene may have only been on the order 100 m/year or less (McLachlan et al. 2005; Petit et al. 2008). While at least some portions of widely-distributed species' ranges should be buffered from these changes in the near term, small-ranged endemics may see conditions deteriorate rapidly and simultaneously across their entire distributions (Thomas et al. 2004; Schwartz et al. 2006), leaving little opportunity for gradual range shifts or natural migration along conservation corridors. For such species, intentional translocation or assisted colonization may be the only option to avoid species extinctions in the wild.

What is the Likelihood of Successful Translocation for Vulnerable TDF Species?

Even if field-based evidence indicated a small-ranged species' decline toward extinction, and assisted colonization was deemed an appropriate response, what is the likelihood that plant species moved beyond their range edges could successfully establish self-maintaining populations in natural communities? Standard biogeographical, paleoecological, and ecological theories suggest that contemporary range edges represent a dynamic equilibrium between environmental conditions, principally climate, and plant population growth rates (Webb 1986; Woodward 1987; Gaston 2003). In the absence of climate change, these 'equilibrial' range models would predict that species translocated beyond their range edges would likely fail to establish (Bellemare 2009). As such, even with anthropogenic climate change, equilibrial range models might suggest that shifts in the distribution of suitable habitat for TDF species might only occur gradually or incrementally. In this scenario, assisted colonization efforts might only be feasible over relatively short distances in the near term (e.g., 10s of km) and might be of questionable value in the long term (e.g., would such translocations actually be repeated in step-like fashion for many decades-centuries?).

However, the applicability of such 'equilibrial' range models to TDF plant species in general, and small-ranged endemics in particular, has recently been called into question (Svenning & Skov 2004; Schwartz et al. 2006; Svenning & Skov 2007a, 2007b; Van der Veken et al. 2007a; Bellemare 2009). Specifically, for species with substantial dispersal limitation, current range boundaries may reflect rather arbitrary positions corresponding to species' dispersal rates, time since last 'disturbance', and distance from past refugia, not fixed positions determined by abiotic limitations to further range expansion (Holt et al. 2005; Svenning & Skov 2007a, 2007b; Bellemare 2009). While the possibility of long-term dispersal limitation of geographic ranges is not widely accepted by paleoecologists (e.g., Webb 1986; Williams et al. 2001; Svenning & Skov 2007a; Van der Veken et al. 2007a), empirical and experimental evidence of such a phenomenon among TDF plant species is increasing (e.g., Holland 1980; Skov & Svenning 2004a; Svenning & Skov 2004b; Van der Veken et al. 2007b;

Bellemare 2009). For example, Bellemare (2009) found that seeds of an ant-dispersed plant, *Jeffersonia diphylla*, successfully germinated and established up to 300 km beyond its current range edge in the northeastern United States. Similarly, Van der Veken et al. (2007b) presented data on an extra-range transplant experiment initiated almost 50 years earlier that showed successful establishment and growth of populations of *Hyacinthoides non-scripta* up to ~ 100 km beyond its natural range edge in northwestern Europe. These studies strikingly illustrate the possibility that for dispersal-limited plant species, the extent of potentially suitable habitat may greatly exceed the area actually occupied, even in the absence of modern climatic changes (Skov & Svenning 2004, Svenning & Skov 2004; Van der Veken 2007a). Such studies suggest that assisted colonization efforts might be feasible over substantially greater spatial scales than would be predicted possible by standard, equilibrial range models.

Another, largely untapped, source of information on assisted colonization's potential scale are the myriad accidental or unplanned 'experiments' undertaken in horticulture, where the climatic limits on numerous plant species' ranges are routinely tested (Van der Veken et al. 2008). Native plants grown for horticultural purposes are commonly grown and propagated well beyond their natural range limits (Van der Veken et al. 2008). The horticultural trade includes many small-ranged TDF endemic species that are commonly grown many 100s to 1000 km or more north of their natural ranges (Braun 1955, Dirr 1998, Cullina 2000, Cullina 2002, Van der Veken et al. 2008). For example, several paleoendemic species associated with the Florida panhandle endemism hotspot in eastern North America, such as *Torreya taxifolia* and *Magnolia ashei*, are grown successfully in regions with much colder and more severe winters, such as in the southern Appalachian Mountains or further north in the northeastern United States (Barlow and Martin 2004; Dirr 1998, Cullina 2002). In

Europe, a recent review by Van der Veken et al. (2008) found that native plants were grown, on average, ~ 1000 km north of their natural range edges in the horticultural trade. While these observations do not provide reliable information on the role that biotic factors (e.g., competitors, pollinators, herbivores, seed dispersers) might play in limiting the ranges of small-ranged plant species in the wild, they do clearly demonstrate that macroclimate *per se* is not limiting for many range-restricted species.

Even stronger evidence for non-equilibrial plant distributions in the TDF biome comes from the many cases where southern TDF endemics introduced for horticulture or forestry have escaped and naturalized in TDF far to the north or west of their natural ranges (Skov & Svenning 2004; Svenning & Skov 2004). For example, many plant species endemic to southern or south-central Europe have been observed to naturalize in the TDF forests of northwestern Europe (e.g., *Aesculus hippocastanum*, *Lilium martagon*, *Aruncus dioicus*, *Eranthis hyemalis*; Lid & Lid 1994; Stace 1997). While such examples have not been as extensively documented in eastern North America, cases of southern species naturalizing in northern areas have been observed (e.g., *Aralia spinosa, Catalpa bignonioides, Robinia pseudoacacia*, *Trillium cuneatum*; Burns & Honkala 1990; Gleason & Cronquist 1991; Case & Case 1997). Such naturalizations suggest that some relatively small-ranged southern species may be capable of establishing and surviving in natural plant communities far to the north of their natural ranges.

The naturalization of southern species in the north may also serve to highlight some of the potential differences between types of endemics and their likelihood of successful translocation. Many of the small-ranged endemic plant species associated with TDF are believed to be paleoendemics that were substantially more widespread in the past (Stein et al. 2000; Estill & Cruzan 2001; Mejías et al. 2002). Apparently through a combination of dispersal limitation and spatial isolation in glacial refugia, many of these species have seemingly failed to recolonize large areas of potentially suitable TDF habitat that have developed during the Holocene (Svenning & Skov 2004a, 2004b; Svenning & Skov 2007a; Van der Veken et al. 2007a). For such paleoendemic species, the probability of successful translocation, even over large geographic scales (e.g., 100s of km), seems high. Indeed, there is the potential for some paleoendemic species to perform better in new areas north of their natural ranges than in the southern refugial areas they currently occupy where climate may already be marginal (e.g., Schwartz 2004; Mejías et al. 2002, 2007). Further, the spatial extent of potentially suitable 'recipient' sites for paleoendemics would appear to be quite large, as TDF is the matrix habitat or potential natural vegetation across large areas of eastern North America and Europe.

In contrast to paleoendemics, neoendemics and ecological endemics appear to be less prevalent in the TDF flora (e.g., Estill & Cruzan 2001); rather, such species are often associated with inclusions of non-forested habitat within the broader TDF biome (e.g., serpentine bedrock, limestone barrens, disturbed areas; Baskin & Baskin 1988, 1989; Estill & Cruzan 2001; Walck et al. 2001). There is a high probability that the distributions of such endemics are limited by factors other than climate (e.g., bedrock or soil type), suggesting that they might tolerate climatic conditions to the north of their current range boundaries, if suitable habitat could be located (e.g., Walck et al. 2001). However, it is also unclear whether these species' climatic tolerances might extend in the other direction as well, meaning that they might be capable of tolerating some degree of climate change *in situ*. Nevertheless, the range of potential recipient sites for ecological endemics and many neoendemics associated with unusual habitats would be considerably more restricted than for TDF-associated paleoendemics. Further, in that the unusual habitat types that might support translocated neo-endemics and ecological endemics are also often spatially limited in the north, and often already harbor rare species, such translocations might be largely precluded by concerns for the ecological sensitivity of such areas.

What are the Ecological Risks for Recipient TDF Communities?

The stated goal of assisted colonization is to preserve biodiversity in the face of rapid climate change; however, is it possible that such intervention might have unintended consequences that negatively impact biodiversity in recipient communities? A number of significant concerns on the ecological risks of assisted colonization have been raised, including the possibility that translocated species might become problematic invasives in their introduced ranges, cause extinctions, or disrupt ecological or economic services provided by recipient ecological communities (Schwartz 2004; Mueller & Hellman 2008; Ricciardi & Simberloff 2009). While these concerns have been well-articulated in the abstract, they have largely been illustrated with examples from a wide range of taxa (e.g., birds, fish, invertebrates) and from widely scattered communities (e.g., lakes, oceanic islands) that may be unrepresentative of plants growing in an extensive continental biome with a long evolutionary history (but see Mueller & Hellman 2008).

Among the concerns expressed regarding assisted colonization, the potential for the creation of new invasive species is most intuitive (Schwartz 2004; Mueller & Hellman 2008; Ricciardi & Simberloff 2009), given the widespread threats posed by biological invasions and the impacts of exotic invasive species on ecological communities (e.g., Mooney and Drake 1986, Mack et al. 2000, Merriam and Feil 2002, Reinhart et al. 2005, Minchinton et al. 2006, Maskell *et al*. 2006). The impacts of introduced species are often unpredictable and may have a range of ecological, biogeochemical, and evolutionary effects, including disruption of existing ecological interactions, competitive exclusion or extirpation of native species, and changes to community-level nutrient cycling dynamics (Ricciardi & Simberloff 2009).

On the other hand, it is unclear how applicable the exotic-invasive paradigm developed in studies of inter-continental and continent-island species invasions would be for intra-continental, intra-biome translocations (Hoegh-Guldberg et al. 2008; Mueller & Hellman 2008). For example, the restricted distributions of some paleoendemics may reflect the species' innate biological limitations on dispersal and population growth; such species would appear unlikely to spread rapidly or become problematic. For other paleoendemics, historical contingency and disjunction from broader areas of suitable habitat may have resulted in the species' limited range size (rather than innate biological characteristics), and initial introduction to new areas could result in successful colonization and substantial rates of subsequent natural range expansion (Mueller & Hellmann 2008).

In terms of species interactions, it is clear that any new species entering a community will engender novel ecological interactions and may modify existing ecological dynamics, even if such effects do not rise to the level of being considered 'invasive' or problematic (Ricciardi & Simberloff 2009). However, in the case of the TDF paleoendemics that might be candidates for assisted colonization, these plant species have been elements of the regional flora for many millions of years, often with fossil records of wider occurrence tracing back through the Tertiary (Mejías et al. 2002; Svenning 2003; Latham & Ricklefs 1993; Manchester 1999). A striking example of this may be provided by *Rhododendron ponticum*, a paleoendemic species whose native range is currently restricted to the Iberian Peninsula and Black Sea-Caucasus region (Mejías et al. 2002). This understory shrub species was introduced to the British Isles via horticulture starting in the 18th century and has subsequently naturalized widely, to the point of being considered a problematic introduced species (Peterken 2001). However, paleoecological evidence documents that *R. ponticum* has been native to the British Isles in previous interglacials and even attained ecological dominance in some Irish forests in a late Middle Pleistocene interglacial (Cross 1975; Coxon 1996). Overall, it seems likely that many paleoendemics have similarly long histories of interaction and co-evolution with the TDF communities of these regions, even if such interactions have been largely absent during the present interglacial. In this sense, the potential for truly ‘novel’ ecological interactions seems low.

The strength and impacts of competitive interactions between native plant species and translocated TDF paleoendemics is unclear and would likely vary considerably based on a range of species-specific characteristics (e.g., plant size and growth rate, habitat preferences, reproductive rate, dispersal mode). However, even if inter-continental species invasions are considered a plausible model for intra-continental translocations, these effects are likely to be limited to moderate for most paleoendemic species that might be translocated. Most exotic plant species introduced to North America and Europe from other continents tend to have limited impacts and exhibit ecological behavior similar to native taxa; indeed, exotic plant species richness is often positively correlated with native plant diversity, especially in forests (Stohlgren et al. 1999; Sax 2002; Deutschewitz et al. 2003, Gilbert and Lechowicz 2005; Stohlgren et al. 2005). Despite serious concerns over the impacts of exotic species, few examples of plant-plant competition causing extinctions have actually been documented (Gurevitch & Padilla 2004; Sax & Gaines 2008). Overall, this suggests that the negative impacts of most exotic plant species on natives are not particularly strong and that many plant communities, including TDF, may not be saturated with species at present (Gilbert & Lechowicz 2005; Stohlgren et al. 2008).

Nevertheless, while most ecological interactions between native plant species and translocated paleoendemics might be predicted to have limited impacts, the potential exists for more substantial effects, especially among paleoendemics that exert strong community-level effects on local environmental conditions (e.g., in terms of light availability, nutrient cycling). For example, tree or shrub species with especially strong effects on understory light levels, nutrient cycling, or evidence of allelopathic effects on understory plants clearly might represent problematic cases. The paleoendemic *Rhododendron ponticum* may illustrate this possibility: where *R. ponticum* has naturalized in forests of the British Isles, light levels in the understory have decreased and understory growth is often suppressed (Cross 1975; Peterken 1996, 2002). Nonetheless, this ecological behavior is by no means unpredictable given the species' dominant role in forests of its native range in the Black Sea-Caucasus region (e.g., Walter and Breckle 1991, Esen et al. 2004); likewise, similar community-level effects of *Rhododendron* species in other TDF regions also stress the potential for strong effects of *R. ponticum* (e.g., *R. maximum* in eastern North America; Nilsen et al. 2001). Overall, this suggests that translocation of paleoendemics with large community-level effects should be avoided or undertaken with considerable caution.

Finally, as a backdrop to concerns about the impacts that the introduction of southern paleoendemics might have on native TDF forest plant communities in the north (e.g., northeastern United States, northern Europe), it should be recognized that the flora and vegetation of these regions are by no means pristine. In the eastern United States, exotic plant species from Eurasia already comprise a substantial percentage of the overall flora (e.g., 30-40% in some regions; Rhoads and Klein 1993, Sorrie 2005; Marks et al. 2008). Similarly, in Europe, the floras of many countries include a large number of non-native species (e.g., ~ 22% in Great Britain, ~ 25% in Germany; Deutschewitz et al. 2003; Chytry et al. 2008). In addition, the majority of TDF vegetation in both eastern North America and Europe has been substantially affected by human activity during the historical period via past agriculture or repeated timber harvesting (Foster et al. 1998; Kirby & Watkins 1998) and the ongoing impacts of pollution and chronic nitrogen deposition still compromise many forest communities (Aber et al. 2003; Van Breemen & Wright 2004). This is not to minimize the significant ecological issues associated with the possibility of assisted colonization (Schwartz 2004; McLachlan et al. 2007; Ricciardi & Simberloff 2009), but rather to place these concerns into a broader ecological and historical context. In this light, we believe that the prospect of preserving paleoendemic plant species for the long term may outweigh concerns over the moderate ecological effects most species might have on recipient communities in the north.

Research Challenges and Opportunities

While assisted colonization may be a reasonable conservation strategy in the future, it is clear that considerable research and investigation are still needed before such efforts could be undertaken. Here we outline some of the major open questions relating to assisted colonization.

First and foremost, considerable research effort is needed to document and monitor existing populations of range-restricted endemics in order to establish a baseline against which future population dynamics can be gauged. Because intervention and translocation should be limited to species demonstrating clear evidence of declines within their native range, basic descriptive research is needed on substantial numbers of species. This may present an opportunity for scientific outreach and 'citizen science', where botanists and plant ecologists could coordinate monitoring activities involving volunteers such as undergraduate biology students, plant enthusiasts, and regional botanical societies.

Because the assumption that plant distributions are in equilibrium with climate (Huntley et al. 1995; Guisan & Thuiller 2005; Schwartz et al. 2006) may not hold for narrow-ranged endemics (Schwartz et al. 2006), new experimental research is urgently needed to directly test the nature of these species' range boundaries. Such efforts might include experimental seed sowing to assess plant performance and its relationship to environmental factors within and beyond range boundaries (e.g., Geber & Eckhart 2005; Van der Veken et al. 2007b; Bellemare 2009). While northern range edges are a clear target for investigation, in light of the probable direction of species future migration or assisted colonization efforts, there is also great need for further insight to the nature of species' southern range boundaries. If, as predicted by some ecological theory (MacArthur 1972), southern range edges are determined by biotic factors rather than climate, there may actually be limited response of species to moderate levels of climate change and assisted colonization may be unnecessary.

Finally, the prospect of intra-specific or ecotypic variation in endemic species suggests that experimental studies testing the nature of range limits should also evaluate population-level differences. It is possible that different ecotypes or subpopulations of endemic species will vary in their performance beyond range edges. For example, ongoing research by Bellemare and Moeller (*unpublished data*) has found that seed germination rates of different populations of the Southern Appalachian paleoendemic *Diphylla cymosa* vary significantly in areas several 100 to 1000 km north of the species' natural range edge in eastern North America. Seeds with the highest germination rate outside the species' range were collected in a population at high elevation within the species' range, suggesting the possibility of greater adaptation or pre-adaptation to colder conditions in this population. Identifying such variation may be key to designing successful conservation efforts and preserving valuable intra-specific diversity in the future.

Conclusions

Temperate deciduous forests represent a widespread and biologically diverse biome in the Northern Hemisphere with a history tracing back through the Tertiary to the late Cretaceous (Wen 1999; Tiffney & Manchester 2001; Willis & McElwain 2002; Wang et al. 2009). These forests have experienced substantial fragmentation and species extinction due to the climatic deterioration of the late Tertiary and Quaternary (Davis 1983; Latham & Ricklefs 1993; Svenning 2003). In the present century, TDF appear to be entering a new phase of climatic challenges with anthropogenic climate warming threatening to compromise the locations of many species' current distributions and drive range shifts to the north or to higher elevation (Delcourt 2002). In eastern North America and Europe, a significant and distinctive component of TDF plant biodiversity is housed in range-restricted, paleoendemic species that are concentrated near the southern margins of the Temperate Zone (Estill & Cruzan 2001; Svenning et al. 2003; Finnie et al. 2007). Many of these paleoendemic species are the last representatives in these regions of ancient TDF plant lineages that were more widespread in the Tertiary; consequently, they represent significant and phylogenetically-distinctive components of regional TDF biodiversity. Substantial biogeographical, paleoecological, and ecological evidence indicates that the distributions of many paleoendemic plant species may not be in close equilibrium with present-day climate, but rather may be relictual in nature, reflecting the locations of glacial-era refugia. These distributional patterns suggest that many paleoendemic species may be both sensitive to rapid climate change and slow to respond to such changes; in addition, the localization of many refugial areas in the south may lead to their being rapidly compromised by anthropogenic climate warming (Hampe & Petit 2005). Given the major climate changes projected for coming decades, empirical and experimental research is urgently needed to better document the effects of changing climate on TDF paleoendemic species and to explore the risks and feasibility of assisted colonization as a conservation strategy. Without such unprecedented conservation actions, the biodiversity and evolutionary legacy of the Temperate Deciduous Forest biome may be severely eroded in the future.

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CHAPTER 4

PROXIMATE ENVIRONMENTAL CORRELATES AND ULTIMATE EVOLUTIONARY SOURCES OF SPECIES RICHNESS GRADIENTS IN TEMPERATE DECIDUOUS FORESTS

Abstract

Ecological theory predicts that species richness in communities should largely represent the outcome of contemporary environmental conditions and local ecological interactions operating over limited spatial and temporal scales. However, evidence is increasing that local diversity patterns may also be influenced by longer-term, larger-scale processes, such as immigration, speciation, and extinction, that influence the numbers of species available to colonize local sites from regional 'species pools'. Here I investigate a prominent plant diversity gradient in Temperate Deciduous Forest to ask whether long-term evolutionary processes, such as phylogenetic niche conservatism and the time available for speciation in different ecological zones, may ultimately explain variation in the numbers of species present along different portions of a key environmental gradient controlling soil fertility: soil calcium content. Analyses of the phylogenetic 'depth' of Temperate Deciduous Forest plant communities along the soil calcium gradient in the northeastern United States indicate that contemporary plant communities with high species richness contain a disproportionate number of taxa from early-diverging angiosperm clades, such as species in the Aristolochiaceae, Lauraceae, and Ranunculaceae. In parallel to these community-level analyses, parsimony-based reconstructions of the ancestral calcium niche for angiosperm lineages documented in the study identify high-calcium soils as a likely ecological zone of origin for angiosperms in Temperate Deciduous Forest

vegetation. Additionally, I find that the relative abundance of plant species in these communities suggests an important role for niche preemption by early-diverging angiosperm lineages, as these taxa often dominate vegetation on sites with fertile, calcium-rich soils. As such, the results of this study highlight the potential for long-term, large-scale evolutionary processes to play a significant role in determining the structure and diversity of contemporary ecological communities.

Introduction

The number of species present in an ecological community may represent the outcome of diverse ecological, biogeographical, and evolutionary processes operating over a wide range of timescales (MacArthur & Wilson 1967; Ricklefs & Schluter 1993; Chesson 2000; Grime 2001; Wiens & Donoghue 2004). However, traditional ecological explanations for variation in species richness among communities or regions have typically focused on dynamics evident at relatively small spatial and temporal scales, such as links between productivity and competition (Grime 1973; Waide et al. 1999), or the impacts of predation and disturbance (Paine 1966; Connell 1978). Nevertheless, there is increasing recognition that longer-term, larger-scale processes, such as species' migration (Svenning & Skov 2007), lineage diversification (Stephens & Wiens 2003), and extinction (Latham & Ricklefs 1993) also need to be considered in explaining the structure and diversity of present-day ecological communities (Ricklefs & Schluter 1993; Zobel 1997; Ricklefs 2006). Indeed, as it is the latter events that ultimately add or subtract species from a region, there is a great need to better integrate such processes into ecological theory (Losos 1996; Zobel 1997; Stephens & Wiens 2003; Ricklefs 2006).

Theories of community assembly and diversity premised on the overriding importance of long-term, large-scale processes have been termed 'species pools' models (Eriksson 1993; Zobel 1997). These models predict that most communities are relatively open to immigration and that differences in species richness among local communities trace to variation in the sizes of regional 'species pools' containing species capable of colonizing a given environmental niche or habitat (Eriksson 1993; Zobel 1997). While sometimes difficult to empirically test (Grace 2001), predictions of these models are often confirmed by comparisons of diversity patterns in different communities within regions, and by comparisons of local communities from different regions with species pools of differing sizes (Ricklefs 1987; Zobel 1997; Pärtel 2002; Ewald 2003). In particular, these analyses suggest that many local communities are not 'saturated' with species, but rather reflect a proportional sampling of regional diversity, such that local diversity is often positively correlated with regional diversity (Ricklefs 1987; Cornell & Lawton 1992). As such, these studies indicate local diversity levels may be linked to long-term, large-scale processes (e.g., migration, diversification, extinction) through their impacts on the sizes of regional species pools (Eriksson 1993; Zobel 1997).

Evidence for the influence of long-term evolutionary processes on species richness may be most apparent when considering diversity gradients among communities or regions (Weins & Donoghue 2004; Ricklefs 2006). In particular, considerable evidence has accumulated that diversity gradients in many taxonomic groups may be underlain by long-term trends in diversification and the relative strength of niche conservatism within lineages (Wiens & Donoghue 2004; Hawkins et al. 2006; Ricklefs 2006; Wiens et al. 2007). For example, regions or ecological zones of origin for a broad range of taxa have been shown to house the greatest diversity of species in these groups, including angiosperm trees (Fine & Ree 2006), New World birds (Hawkins et al. 2006), marine bivalves (Jablonski et al. 2006), and tropical salamanders (Wiens et al. 2007). In contrast, more recently colonized regions or ecological zones typically include fewer and more recently-derived species (Wiens & Donoghue 2004; Hawkins et al. 2006; Ricklefs 2006). While the results of these studies confirm the critical role of present-day environmental gradients or abiotic factors as proximate correlates of biodiversity, they emphasize that the ultimate cause or source of many species richness gradients may be the time available for speciation in different regions or ecological zones (i.e., 'time-for-speciation effect' of Stephens & Wiens 2003; Ricklefs 2006). These new evolutionary insights to long-standing questions in ecology (e.g., latitudinal diversity gradients) promise to extend and enhance the explanatory power of ecological theory in coming years (Losos 1996; Webb et al. 2002; Ricklefs 2006).

Beyond simple counts of the numbers of species present in communities, ecological theory also seeks to elucidate the processes underlying a range of community-level characteristics, including patterns of species' relative abundances, dominance, and co-occurrence (MacArthur 1960; Rabinowitz 1981; Brown 1984; Keddy & Shipley 1989; Grime 2001). While the role of longer-term, larger-scale processes in these more complex intra-community patterns have been less thoroughly explored, there are indications that such patterns may also be influenced by 'deep history' (Wilson 1961; DiMichele et al. 2001; Ricklefs 2005; Vitt & Pianka 2005). For example, evidence for phylogenetic niche conservatism in numerous plant and animal taxa (Peterson et al. 1999; Prinzing et al. 2001; Hawkins et al. 2006) suggests that many lineages are restricted to portions of the environment inhabited by their ancestors (i.e., their 'ancestral niche') and may only occasionally colonize new ecological zones. At the community level, such niche conservatism appears to be exemplified in the long-term stasis in composition and structure of many ancient plant and animal communities (Brett et al. 1996; Miller 1996; DiMichele et al. 2001), with only infrequent periods of rapid change, species turnover, and substantial niche shifts or expansion documented in the fossil record. Taken as a whole, these patterns seem to indicate that dynamics at crucial periods in the distant past (e.g., following mass extinctions, faunal or floristic turnovers, rapid climate change) may exert a long-standing influence on the structure of ecological communities (Brett et al. 1996; Vitt & Pianka 2005). In particular, it is hypothesized that ecological processes operating during or soon after such events, including niche preemption with the advent of new ecological opportunities or species sorting due to preadaptation to novel conditions, may have lasting consequences for community structure and diversity (Simpson 1953; Brett et al. 1996; Ackerly 2004).

In this study, I investigate a prominent plant species diversity gradient to ask whether long-term, large-scale processes, such as phylogenetic niche conservatism, might explain variation in species richness along a prominent environmental gradient. In particular, I focus my analyses on variation in the species richness of angiosperm plant communities along a soil fertility gradient in Temperate Deciduous Forest (TDF). This vegetation type has a long history in the Northern Hemisphere and includes a diverse array of angiosperm lineages, making it an ideal system to investigate the potential for past evolutionary processes to drive ecological patterns in present-day communities. In addition, prior studies have shown that species richness in TDF plant communities varies strongly with soil pH and calcium content, two correlates of overall soil fertility (Chytry et al. 2003; Peet et al. 2003; Bellemare et al. 2005). However, the evolutionary processes that might ultimately drive this diversity gradient have not been convincingly demonstrated and most interpretations have focused on proximate environmental correlates, such as site ‘favorability’ to plants (Peet et al. 2003; Bellemare et al. 2005).

Thus, this study specifically addresses the following issues: First, I examine the nature of the relationship between angiosperm species richness and soil calcium to test for evidence of community saturation or competitive exclusion at high soil fertility. Specifically, local dynamics of this nature might be expected to produce a plateau or decline in species richness on fertile, high-calcium soils due to competitive exclusion. Second, I use the distribution of naturalized exotic plant species as an 'unplanned experiment' (Sax et al. 2007) to test for the relative openness of TDF plant communities to colonization. Community models premised on the importance of local interactions might predict greater resistance of species-rich communities to invasion (Elton 1958), whereas species pools models predict that most communities are relatively open to immigration. Third, I use estimates of mean phylogenetic 'depth' in TDF plant communities along the soil calcium gradient and reconstructions of angiosperm lineages' ancestral calcium niches to ask whether ecological zones with a longer history of occupation support communities with greater species richness (c.f., Hawkins et al. 2006; Ricklefs 2006). Specifically, if long-term evolutionary processes, such as phylogenetic niche conservatism, contribute to the contemporary gradients in species diversity, it is predicted that species-rich communities should exhibit greater mean phylogenetic depth than species-poor communities, and that species-rich communities should be centered on environmental conditions corresponding to the focal lineage's ecological zone of origin (Ricklefs 2006). Finally, I investigate aspects of intra-community structure along the soil calcium gradient to ask whether contemporary patterns of abundance and dominance are suggestive of evolutionary or ecological dynamics in 'deep history', such as niche preemption by early diverging lineages.

Methods

Study System and Study Area

Temperate Deciduous Forests (TDF) are found primarily in three disjunct regions of the Northern Hemisphere: eastern North America, Europe, and eastern Asia (Wen 1999; Donoghue & Smith 2004). While widely separated today, the TDF communities of these regions share a common evolutionary and biogeographical history tracing to the Tertiary, when moderate climatic conditions and greater interconnection between Eurasia and North America allowed for the development of mesophytic forest communities across large areas of the Northern Hemisphere (Wen 1999; Donoghue & Smith 2004). Despite many millions of years of subsequent separation, these disjunct TDF plant communities still exhibit great similarity in terms of physiognomy and floristic composition at the family and generic level (White 1983; Wen 1999; Donoghue & Smith 2004). In this study, I focus on forest plant communities in a region where TDF is well-represented: the northeastern United States. Due to its heterogeneous geology, this region is characterized by substantial variation in soil calcium content (Bellemare et al. 2005), thus allowing for a comprehensive analysis of the correlation between this prominent environmental gradient and TDF plant species richness and community phylogenetic structure.

Characterization of Vegetation and Environment

Temperate Deciduous Forest vegetation was sampled in fifty 0.1 ha plots (20 x 50 m) located at sites across the northeastern United States (Figure 4.1). Sites were selected for inclusion based on two criteria: site history and environmental setting. In terms of site history, only forest stands that were well-developed (e.g., included relatively large, forest-grown trees) and lacked signs of substantial past human disturbance (e.g., agricultural land-use) were sampled. A number of the sites included had previously been identified as ‘old growth’ or ‘ancient forest’ (e.g., Kershner & Leverett 2004). In cases where such prior designations had not been made, field evidence was used to determine that the sites had likely been forested throughout the historical period (i.e., ‘primary forest’ *sensu* Peterken 1996), although some woodcutting or other non-agricultural human disturbance may have taken place in the past. In terms of environmental setting, sites were selected so as to include a broad gradient of soil nutrient and fertility conditions, stretching from sites on calcium-rich, circumneutral soils through sites on calcium-poor, acidic soils. This was accomplished through the targeted selection of forest sites occurring on a range of bedrock types with differing chemical composition (e.g., calcium-rich limestone vs. calcium-poor schist), and across sites with differing surficial geologies (e.g., relatively fine-textured glacial till vs. coarse-textured glacial outwash).

Within each site, 1-2 randomly placed 0.1 ha plots were established to sample vegetation and environmental characteristics. Summer-green vegetation was surveyed in these plots during the period from June through August, in 2005-2008. Within each plot, all vascular plant species growing in the ground layer (≤ 1 m height) were identified and their cover (%) was estimated using a 10-point cover class scale developed by the North Carolina Vegetation Survey (Peet et al. 1998). The status of species as native or exotic was determined following Gleason and Cronquist (1991). To characterize soil chemistry and nutrient status, four mineral soil samples (0-10 cm depth) were collected from each plot using a polyvinyl chloride (PVC) corer with an inside diameter of 5.3 cm (total volume ~ 221 cm^3). Soil samples were oven-dried for48 hours at 50° C prior to being sieved to ≤ 2 mm. The four samples from each plot were subsequently pooled, homogenized, and submitted to Brookside Laboratories, Inc. (New Knoxville, OH) for analysis of a variety of physical and chemical properties, including soil texture, organic matter content, pH, and cation concentrations (e.g., calcium concentration).

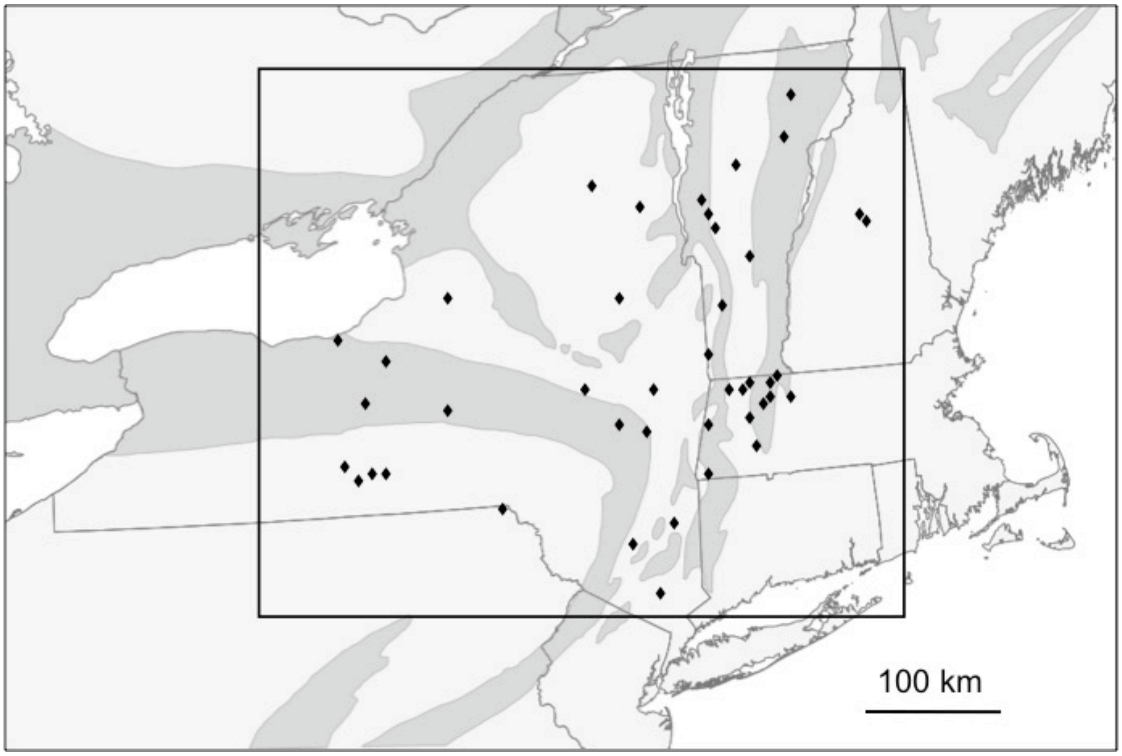


Figure 4.1. Locations of fifty 0.1 ha vegetation plots sampled in Temperate Deciduous Forest across the northeastern United States (black diamonds) and their distribution relative to calcium-rich bedrock types in the region (gray shading). Sites that included two plots are not differentiated from single plot sites here.

Phylogenetic Depth of Species and Communities

For each angiosperm plant species recorded in the vegetation survey, I calculated an estimate of phylogenetic 'depth' by determining the number of nodes separating the species' family from the root of the angiosperm phylogenetic 'supertree' presented in Davies et al. (2004). Family designations for species followed current taxonomy as indicated in the USDA PLANTS database (http://plants.usda.gov/); however, these familial assignments were then standardized to follow the family classification recognized by APG II (Angiosperm Phylogeny Group 2003) and utilized by Davies et al. (2004). With this approach, taxa in early-diverging or 'basally-derived' families that are separated by fewer nodes from the root of the angiosperm supertree are considered to exhibit greater phylogenetic depth; in contrast, later-diverging or more 'recently-derived' families that are separated from the angiosperm root by a greater number of nodes are considered to exhibit lesser phylogenetic depth. While using direct estimates of the ages of angiosperm families (e.g., Wikström et al. 2001) would be an alternative approach to estimating phylogenetic 'depth', such age estimates involve considerably greater uncertainty and are prone to substantial revision with new molecular or fossil data (Anderson et al. 2005). More importantly, the evolutionary patterns of interest (e.g., niche conservatism, major niche shifts) are expected to be associated with significant cladogenic events (i.e., nodes on a phylogeny), not time or lineage age *per se* (i.e., branch lengths on a phylogeny).

Using species-level estimates of phylogenetic depth, I calculated a 'Mean Community-level Phylogenetic Depth' score (MCPD) for each plot by determining the average phylogenetic depth of all angiosperm species present in the plot. To incorporate aspects of community structure into estimates of phylogenetic structure, I also calculated an 'Abundance Weighted Mean Phylogenetic Depth' score (AWPD) for each plot. In this case, I determined the abundance (i.e., % cover) of individual angiosperm species relative to the total cover of angiosperm plant species in each plot; these relative or proportional abundances were then used to weight estimates of community-level mean phylogenetic depth. Taken together, these two estimators of community-level phylogenetic depth should provide insight to the phylogenetic structure of plant communities (MCPD score) and to intra-community ecological patterns of abundance and dominance (AWPD score).

Species Richness, Community Phylogenetic Depth, and Soil Calcium

Linear regression was used to evaluate the strength and form of the association between soil calcium content and angiosperm species richness in the vegetation plots. Both variables were natural-log transformed prior to analysis to meet assumptions of normality. The relationship between the number of native and introduced exotic angiosperm species was plotted and visually inspected, although numerous zero values for exotic species richness precluded regression analysis. Linear regression was also used to evaluate relationships between community-level phylogenetic structure (i.e., MCPD and AWPD) and soil calcium content. All statistical analyses were conducted in JMP 7.0.2 (SAS Institute, Cary, NC).

Calcium Niche Evolution and Ecological Zones of Origin

An abundance-weighted mean calcium niche position was calculated for each angiosperm family encountered in the vegetation plots. This was done by determining the total summed cover of species in each family across all 50 plots, and then using this value to calculate the proportion of a family's total cover represented by its occurrence in an individual plot; this proportion was then used to weight calculations of the mean calcium content of soils where the family occurred. These calcium niche values were then converted from a continuous scale to 3 distinct character states: low soil calcium niche (0-999 calcium ppm), moderate calcium niche (1000-1999 ppm), and high calcium niche (2000+ ppm). These character states were mapped onto a phylogenetic supertree including all angiosperm families encountered in the plots; resolution of the phylogeny followed APG II (Angiosperm Phylogeny Group 2003) and Davies et al. (2004). Parsimony analysis in MacClade 4.0 (Maddison & Maddison 2000) was used to reconstruct ancestral character states and to draw inferences on the ecological zone of origin for angiosperm clades present in TDF vegetation. Importantly, as calcium niche data were only available for taxa encountered in the present study, taxon sampling is incomplete and character reconstructions should be interpreted cautiously.

Results

Species Richness and the Soil Calcium Gradient

Across the 50 plots sampled, over 320 angiosperm species were identified in ground layer vegetation, including taxa in 63 families. Angiosperm species richness varied almost 7-fold across the plots, with a minimum of 15 and a maximum of 101 species documented per 0.1 ha; mean species richness was 46.4 (± 2.9 SE). In terms of the edaphic environment, calcium was the most abundant soil cation in plots with soils of moderate acidity to circumneutral pH (e.g., pH 5.0-7.5), where calcium content averaged 2957 ppm and Ca^{2+} comprised ~ 63% of total cations. On sites with more acidic soils (e.g., 3.7-4.8), calcium content averaged 571 ppm and Ca^{2+} comprised only ~ 24% of total cations, being surpassed by H^+. Species richness showed a highly significant monotonically positive relationship with soil calcium content ($F_{1,48} = 97.78$, $p < 0.0001$, $R^2 = 0.67$; Table 4.1; Figure 4.2, 4.3). Notably, the highest species richness (101 spp) was documented in the plot with the highest soil calcium content (8003 ppm or 91% of total cations). The species richness of native and exotic angiosperms was strongly positively correlated (Figure 4.4).

Community Phylogenetic Depth and the Soil Calcium Gradient

The phylogenetic depth of individual angiosperm species encountered in the vegetation plots varied substantially. Family nodal depths ranged from a low of 8-12 nodes among species in basally-derived angiosperm lineages (e.g., Aristolochiaceae, Lauraceae) and early-diverging Lower Eudicot taxa (e.g., Papaveraceae, Ranunculaceae), to a high of 27-35 nodes among species in more phylogenetically-derived Core Eudicot lineages (e.g., Asteraceae, Lamiaceae, Verbenaceae). When averaged across all the angiosperm species present in a plot to calculate Mean Community-Level Phylogenetic Depth (MCPD), values for MCPD scores ranged from a low of 19.2 to a high of 23.1, with an average of 21.0 (± 0.1).

Plot MCPD scores were significantly negatively correlated with soil calcium content ($F_{1,48} = 10.5235$, $p = 0.0021$, $R^2 = 0.18$; Table 4.2; Figure 4.5), meaning that plots with calcium-rich soils had a greater proportional representation of species from basally-derived or early-diverging angiosperm families (i.e., fewer nodes to root of angiosperm supertree). In particular, representatives of Basal Angiosperm lineages, such as *Asarum canadense* (Aristolochiaceae; 9 nodes to root) and *Lindera benzoin* (Lauraceae; 12 nodes), and early-diverging Lower Eudicot lineages, such as *Caulophyllum thalictroides* (Berberidaceae; 12 nodes) and *Actaea pachypoda* (Ranunculaceae; 12 nodes) were frequent components of plant communities on calcium-rich soils. In contrast, TDF plant communities on soils of low to moderate calcium content typically lacked these species and were composed primarily of species from more recently-derived lineages, such as *Vaccinium* spp. (Ericaceae; 24 nodes) or *Viburnum* spp. (Caprifoliaceae; 20 nodes). While these shifts in vegetation composition also coincided with changes in the growth form of ground layer plants

Table 4.1. Linear regression of angiosperm species richness on soil calcium content across fifty 0.1 ha plots in Temperate Deciduous Forest vegetation in the northeastern United States. Soil calcium content (parts per million) and species richness were natural-log transformed prior to analysis. See also Figure 4.2, bottom panel.

Source	Degrees of freedom (df)	Sum of Squares (SS)	Mean Square (MS)	F-ratio	p-value
Regression	1	6.64026	6.64026	97.7772	< 0.0001
Residual	48	3.25979	0.06791		

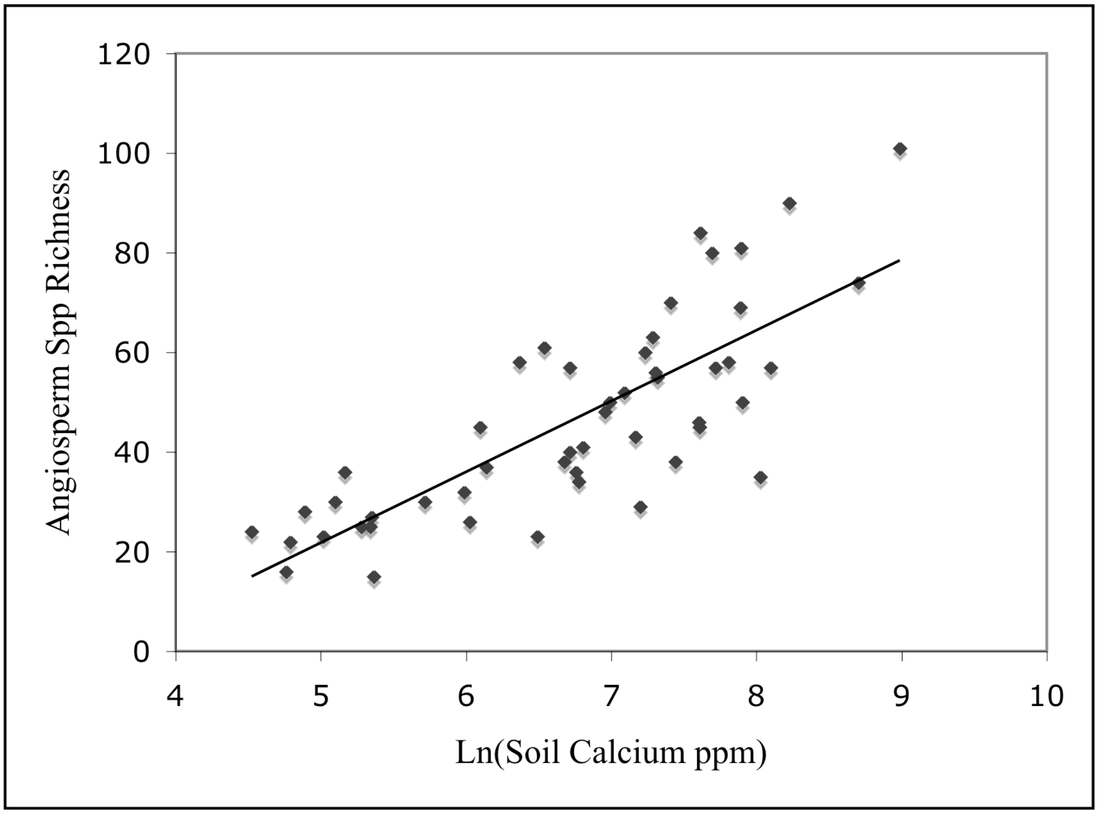


Figure 4.2. The relationship between natural log-transformed soil calcium content (ppm) and angiosperm species richness in ground layer vegetation of Temperate Deciduous Forests sampled in fifty 0.1 ha plots across the northeastern United States. This figure is included for interpretive purposes; regression analysis was conducted on natural-log transformed species richness, see Figure 4.3. Note truncated x-axis.

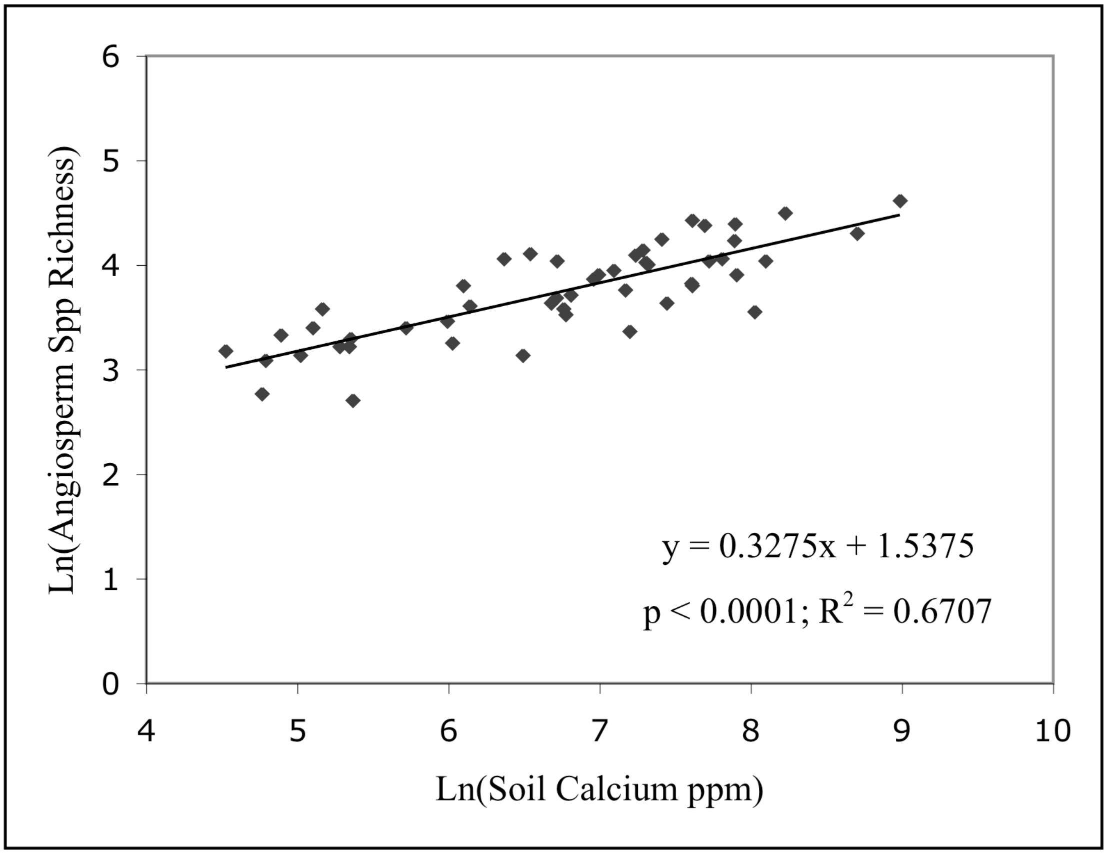


Figure 4.3. Linear regression of natural log-transformed angiosperm species richness on natural log-transformed soil calcium content (ppm) in ground layer vegetation of Temperate Deciduous Forests sampled in fifty 0.1 ha plots across the northeastern United States. Note truncated x-axis.

(e.g., from predominantly herbaceous species on calcium-rich soils to predominantly woody species on calcium-poor soils), it is notable that most woody Basal Angiosperm and Lower Eudicot species did occur on calcium-rich soils (e.g., *Liriodendron tulipifera* and *Magnolia acuminata* in Magnoliaceae, 11 nodes to root; *Lindera benzoin* in Lauraceae, 12 nodes; *Menispermum canadense* in Menispermaceae, 11 nodes). In contrast, many herbaceous members of more recently-derived Core Eudicot lineages were associated with calcium-poor soils (e.g., *Oxalis acetosella*, Oxalidaceae, 21 nodes; *Trientalis borealis*, Primulaceae, 23 nodes).

Estimates of community-level phylogenetic depth that incorporated species' relative abundances also showed a significant trend relative to soil calcium content. As with MCPD, Abundance Weighted Mean Community-Level Phylogenetic Depth (AWPD) was significantly negatively correlated with soil calcium content ($F_{1,48} = 17.6982$, $p = 0.0001$, $R^2 = 0.27$; Figure 4.6). This implied that, in general, both the number and relative abundances of basally-derived and early-diverging angiosperm families in TDF vegetation increased on calcium-rich soils relative to vegetation on calcium-poor soils. While the association between AWPD and soil calcium appeared to be stronger than the correlation between MCPD and soil calcium (i.e., lower p value, higher R^2), a pattern of increasing variability in AWPD at high soil calcium concentrations was also evident. While this heteroscedasticity may reduce confidence in the statistics derived from the regression analysis, this pattern of increasing variability in AWPD at high calcium appears to reflect a real biological phenomenon, whereby the ground layer vegetation of some sites with calcium-rich soils is dominated by early-diverging taxa, while at other calcium-rich sites, more recently-derived taxa were co-dominant or dominant relative to earlier-diverging taxa. In contrast, the vegetation of calcium-poor sites was not observed to include a substantial component of basally-derived or early-diverging angiosperm lineages in any case,

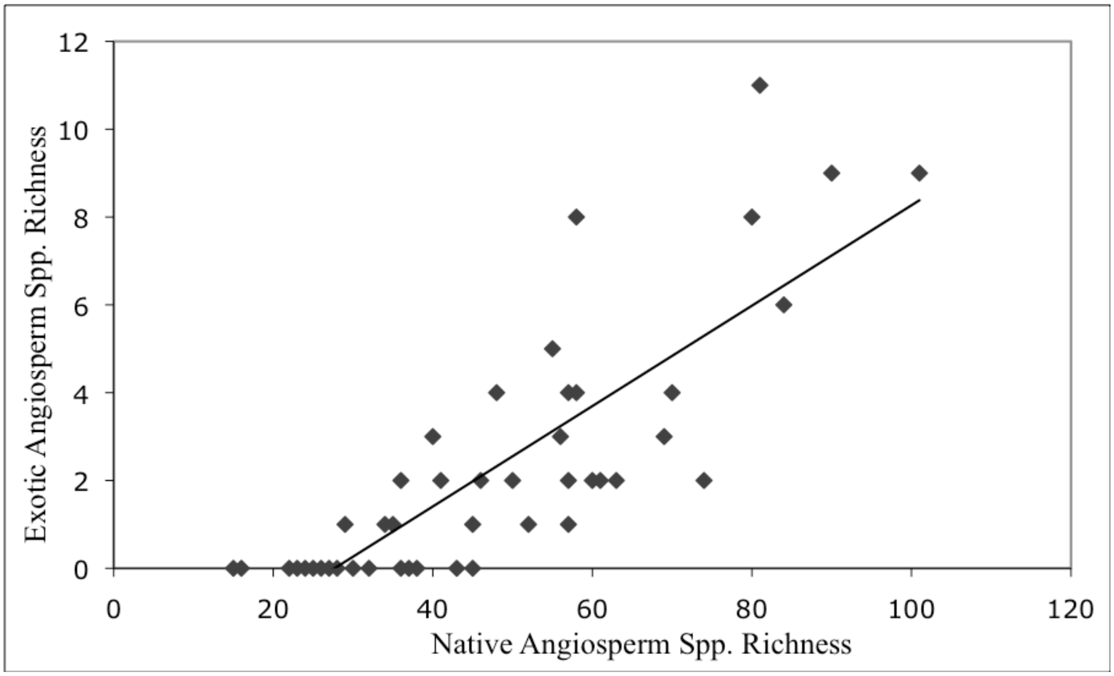


Figure 4.4. The relationship between native and exotic angiosperm species richness in ground layer vegetation of Temperate Deciduous Forests sampled in fifty 0.1 ha plots across the northeastern United States. Regression analysis was precluded by the high number of observations (plots) with zero exotic species; however a linear trend is evident and highlighted here.

Table 4.2. Linear regression of Mean Community-Level Phylogenetic Depth (MCPD) on soil calcium content across fifty 0.1 ha plots in Temperate Deciduous Forest vegetation in the northeastern United States. Soil calcium content (parts per million) was natural-log transformed prior to analysis. See also Figure 4.6.

Source	Degrees of freedom (df)	Sum of Squares (SS)	Mean Square (MS)	F-ratio	p-value
Regression	1	5.283299	5.28330	10.5235	0.0021
Residual	48	24.098189	0.50205		

leading to lower variability and uniformly higher AWPD scores (Figure 4.6).

Calcium Niche Evolution and Ecological Zones of Origin

Angiosperm plant families varied widely in the position of their abundance-weighted calcium niche, with some taxa restricted almost entirely to sites with relatively high calcium soils (e.g., Berberidaceae), while others occupied only low calcium soils (e.g., Ericaceae). When mapped onto the phylogenetic supertree including the 63 angiosperm families encountered in the vegetation plots, these data led to a reconstruction of ancestral calcium niches (i.e., ancestral character states) suggesting an important role for calcium-rich soils in the early evolution of angiosperms (Figure 4.7). In particular, the ancestor of the angiosperm clade including Basal Angiosperms and the Eudicots was inferred to inhabit calcium-rich soils. In contrast, the ancestor of the sister group to this clade, the Monocots, was inferred to inhabit soils of moderate calcium concentration (Figure 4.7).

Discussion

Temperate Deciduous Forests are characterized by significant intra-regional gradients in species richness associated with soil calcium content. While previous studies have documented these patterns in a number of regions, explanations for this plant diversity gradient have generally been limited to correlations with proximate environmental factors or local ecological processes (e.g., soil fertility, productivity). The results of the present study demonstrate that, while plant diversity is strongly correlated with environmental factors (i.e., soil calcium content), this ecological pattern may ultimately be driven by long-term trends in the evolution and diversification of angiosperms in the Temperate Zone.

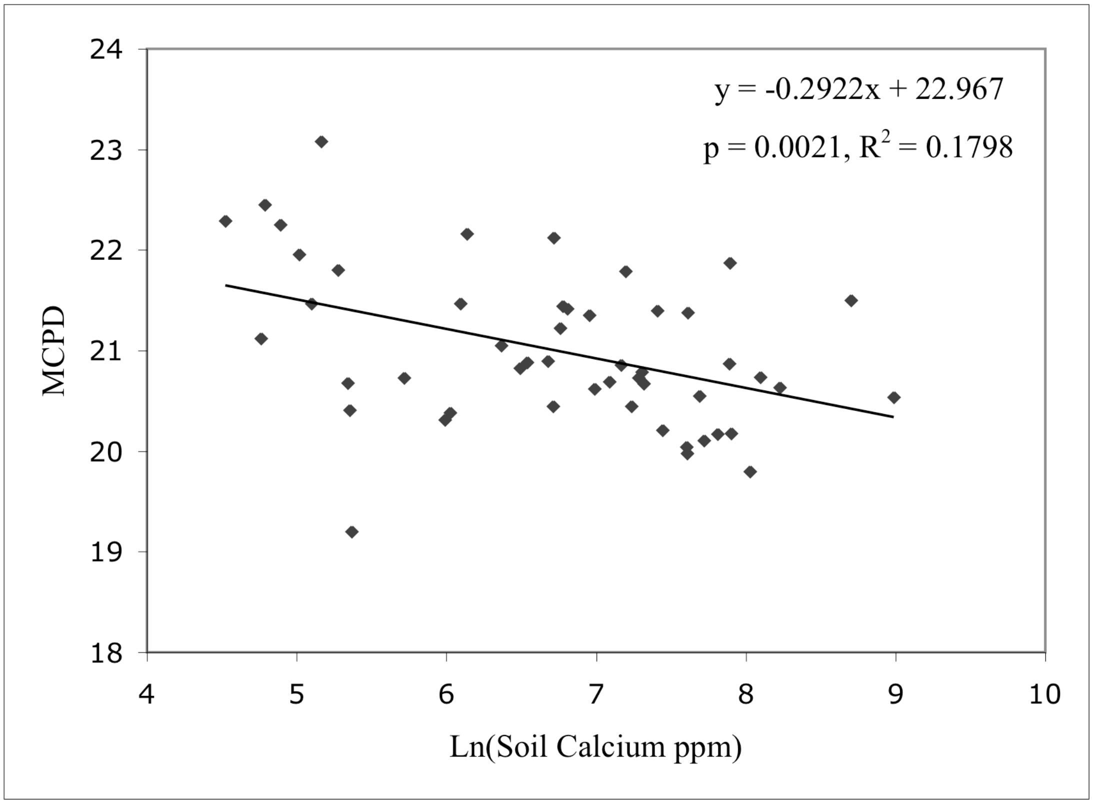


Figure 4.5. The relationship between soil calcium content (ppm) and Mean Community-Level Phylogenetic Depth (MCPD) in ground layer angiosperm plant communities of Temperate Deciduous Forests sampled in fifty 0.1 ha plots across the northeastern United States. Soil calcium content was natural-log transformed prior to analysis. Note truncated y- and x-axes.

The analyses detected little evidence for community saturation or local competitive interactions in limiting species richness in TDF; rather, these plant communities appear relatively open to colonization by new immigrants entering regional species pools (e.g., recently introduced exotic plants). As such, differences in species richness among communities along this important environmental gradient are likely to reflect variation in the number of species present in regional 'species pools' capable of establishing along different portions of the soil calcium gradient. The analyses of community phylogenetic depth and reconstructions of angiosperm lineages' ancestral calcium niche suggest that the ultimate source of this variation in species pool sizes may be phylogenetic niche conservatism, whereby many extant angiosperm species are still associated with ecological zones occupied by their ancestors. Finally, the results of this study also suggest that niche preemption or'incumbency' by ancient, early-diverging angiosperm lineages may be a key factor structuring relative abundance patterns in some present-day TDF plant communities.

Species Richness, Community Saturation, and the Soil Calcium Gradient

This study's finding of a significant, monotonically-increasing correlation between soil calcium content and species richness provides little evidence for community saturation or competitive exclusion in TDF plant communities on fertile soils (Figures4.2, 4.3). This conclusion is reinforced by the positive correlation apparent between native and exotic species richness (Figure 4.4), suggesting that even the most species-rich TDF plant communities are relatively open to colonization by new immigrants; indeed the high species richness of some of these communities includes a notable component of introduced taxa (e.g., 3-14% in communities with 70 or more

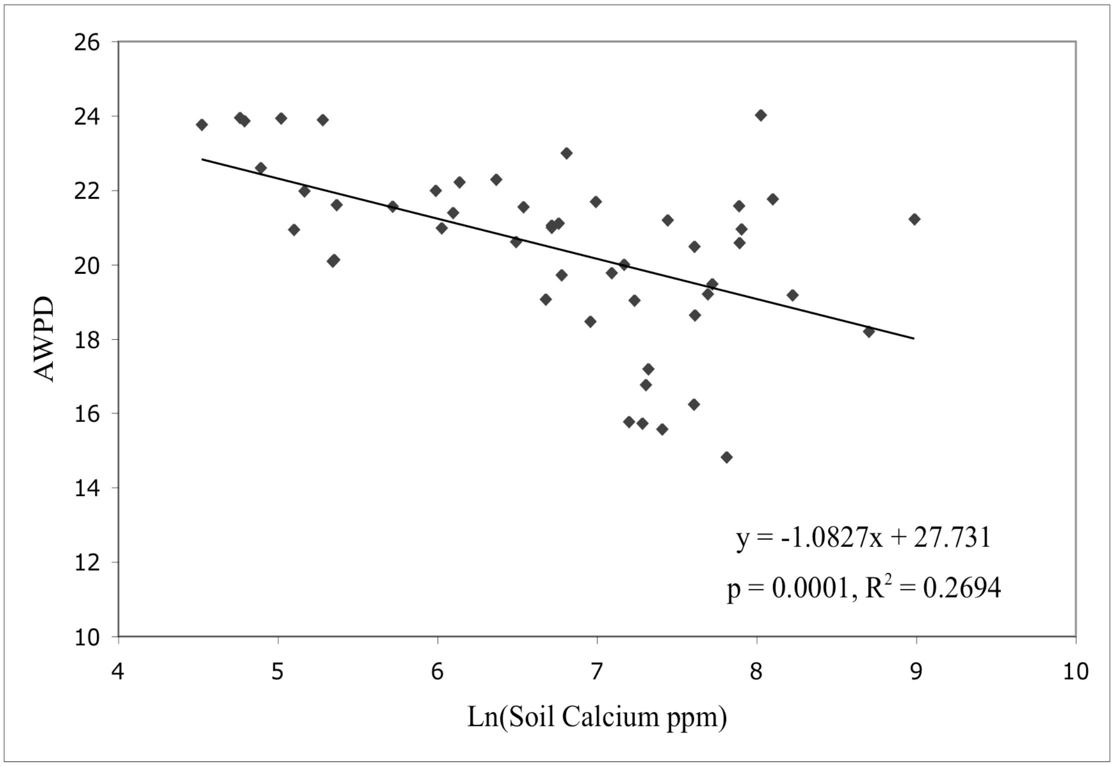
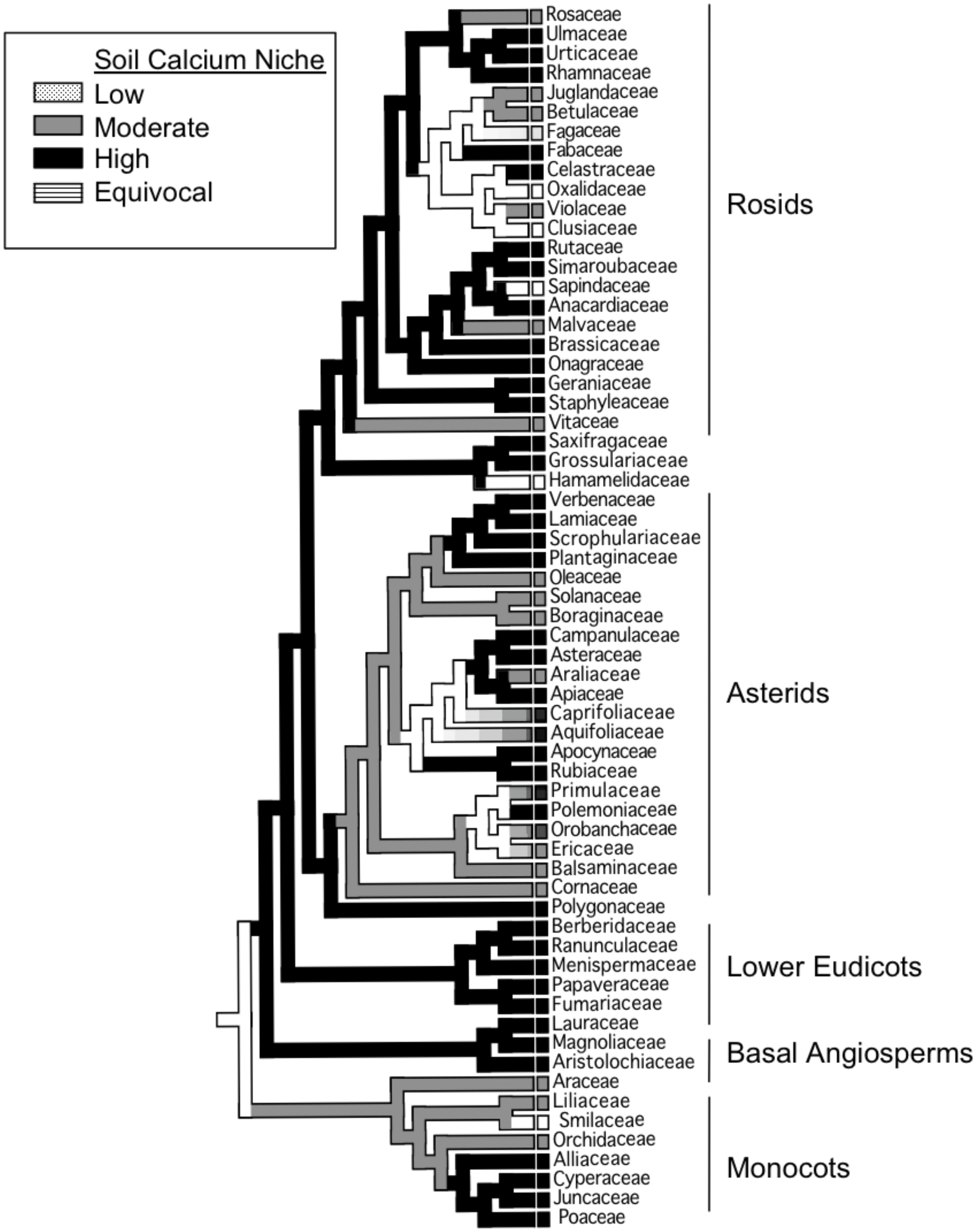


Figure 4.6. The relationship between soil calcium content (ppm) and Abundance Weighted Mean Phylogenetic Depth (AWPD) in ground layer angiosperm plant communities of Temperate Deciduous Forests sampled in fifty 0.1 ha plots across the northeastern United States. Note truncated y- and x-axes.

angiosperm species). Overall, these findings are consistent with previous studies that have documented similar positive correlations between soil calcium (or soil pH) and plant species richness in TDF in other parts of the eastern United States (e.g., Peet et al. 2003) and in TDF in Europe (e.g., Chytry et al. 2003; Borchsenius et al. 2004). Likewise, other studies have documented positive correlations between native and exotic species richness in TDF (e.g., Gilbert & Lechowicz 2005). Explanations for this calcium-associated diversity gradient typically invoke increased 'favorability' of calcium-rich soils for plant establishment and growth (Peet et al. 2003; Bellemare et al. 2005), as soil calcium concentration is positively correlated with a range of edaphic factors determining soil fertility (Brady 1990). In particular, calcium concentration influences soil pH through Ca^{2+} displacement of H^+ on cation exchange sites in soil, allowing for greater retention of Ca^{2+} and other elemental plant nutrients (Brady 1990). Additionally, increased soil pH and calcium concentration have been linked to greater rates of N mineralization and nitrification in forest soils, increasing N availability to plants (Goodale & Aber 2001; Christopher et al. 2006). However, while such environmental conditions might favor greater productivity and higher plant growth rates on sites with higher soil calcium content, the causes of higher species richness are still ambiguous. In particular, a considerable body of ecological theory predicts that high soil fertility and plant community productivity may lead to *declines* in species richness due to local competitive exclusion (i.e., unimodal or hump-shaped productivity-diversity relationships; Grime 1973; Waide et al. 1999). As such, the increased species richness of TDF plant communities on calcium-rich, high-pH soils begs further explanation.

Figure 4.7. The abundance-weighted soil calcium niche of angiosperm families in ground layer vegetation of Temperate Deciduous Forests sampled in fifty 0.1 ha across the northeastern United States. The calcium niche of extant taxa is categorized to 3 character states: low calcium (0-999 ppm), moderate (1000-1999), and high (2000+). Character states for ancestral taxa were inferred from extant taxa included in this study using parsimony analysis in MacClade 4.0. Major angiosperm clades are indicated in italics (right).


Soil Calcium Niche
Low
Moderate
High
Equivocal
Rosaceae
Ulmaceae
Urticaceae
Rhamnaceae
Juglandaceae
Betulaceae
Fagaceae
Fabaceae
Celastraceae
Oxalidaceae
Violaceae
Clusiaceae
Rutaceae
Simaroubaceae
Sapindaceae
Anacardiaceae
Malvaceae
Brassicaceae
Onagraceae
Geraniaceae
Staphyleaceae
Vitaceae
Saxifragaceae
Grossulariaceae
Hamamelidaceae
Verbenaceae
Lamiaceae
Scrophulariaceae
Plantaginaceae
Oleaceae
Solanaceae
Boraginaceae
Campanulaceae
Asteraceae
Araliaceae
Apiaceae
Caprifoliaceae
Aquifoliaceae
Apocynaceae
Rubiaceae
Primulaceae
Polemoniaceae
Orobanchaceae
Ericaceae
Balsaminaceae
Cornaceae
Polygonaceae
Berberidaceae
Ranunculaceae
Menispermaceae
Papaveraceae
Fumariaceae
Lauraceae
Magnoliaceae
Aristolochiaceae
Araceae
Liliaceae
Smilaceae
Orchidaceae
Alliaceae
Cyperaceae
Juncaceae
Poaceae
Rosids
Asterids
Lower Eudicots
Basal Angiosperms
Monocots

The monotonic positive relationship seen between species richness and soil calcium in TDF, and the positive correlation apparent between native and exotic plant richness in these communities, has led a number of researchers to step back from hypotheses premised on local, short-term ecological controls on species richness to consider longer-term, larger-scale processes (Ewald 2003; Gilbert & Lechowicz 2005). For example, in analyses of species richness patterns in European vegetation, Pärtel (2002) and Ewald (2003) have proposed that the higher species richness of plant communities on high pH soils might trace to the varying sizes of the regional species pools associated with these habitats. In particular, Ewald (2003) suggested that the contraction and marginalization of the European TDF flora to southern areas with predominantly calcareous soils during the Pleistocene might have led to the increased extinction of acid soil-preferring, 'calcifuge' plant species, resulting in a modern flora skewed toward 'calciphile' plant species. While such a phenomenon seems plausible in the European context, Peet et al. (2003) have noted that similarly strong trends toward higher species richness on calcium-rich soils are evident in the TDF of the Southern Appalachians of eastern North America, where calcareous soils and bedrock are relatively uncommon and the locations of putative Pleistocene refugia do not appear to be biased toward areas with calcium-rich soils. Accordingly, Pleistocene extinctions appear unlikely to explain the contemporary intra-regional diversity gradient associated with soil calcium. While Peet et al. (2003) concluded that such patterns are likely driven by present-day environmental factors, including site 'favorability' to plants, they also noted that genus- and family-diversity increased with pH and calcium, potentially 'suggesting an ancient origin for this pattern'. The results of the present study strongly support the latter possibility.

Community Phylogenetic Depth, Ecological Zones of Origin, and Soil Calcium

The phylogenetic depth of TDF plant communities increased significantly along the soil calcium gradient, driven by a greater proportional representation of Basal Angiosperm and Lower Eudicot taxa on calcium-rich sites, and the general absence of such species on calcium-poor sites. The restriction of basally-derived and early-diverging angiosperm lineages to calcium-rich soils, together with the higher species-richness of plant communities on these soils, is strongly suggestive of an important role for phylogenetic niche conservatism or a time-for-speciation effect in driving present-day diversity patterns in TDF (cf. Stephens & Wiens 2003; Hawkins et al. 2006; Ricklefs 2006). Specifically, while representatives of more recently-derived lineages (e.g., Core Eudicots) are just as 'old' as extant representatives of early-diverging, basally-derived sister clades (e.g., some Basal Angiosperms, Lower Eudicots), it is hypothesized that basally-derived lineages that have undergone comparatively less cladogensis subsequent to their divergence should retain ecological and biological traits similar to the common ancestor of the clade in question (cf. Field et al. 2004). As such, the association of Basal Angiosperm and Lower Eudicot taxa with calcium-rich soils suggests that the ancestral niche or ecological zone of origin for this clade (i.e., Basal Angiosperms + Lower Eudicots + Core Eudicots) was centered on calcium-rich soils. It is in such ecological zones of origin that researchers predict the highest species richness for a clade (Ricklefs 2006). These community-based inferences to the ancestral niche of the Basal Angiosperms and Eudicots are also reinforced by the results of calcium niche character mapping and reconstruction. Specifically, based on the data set including calcium niche estimates for 63 angiosperm families, I inferred that the ancestral niche or ecological zone of origin for the clade including Basal Angiosperms and Eudicots was on calcium-rich soils (Figure 4.7).

The restriction of most extant Basal Angiosperm and Lower Eudicot taxa in TDF to calcium-rich soils suggests that long-term phylogenetic niche conservatism may be a critical factor determining their contemporary distributions. While more recently-derived lineages have colonized other portions of the soil calcium gradient, indicating the potential for niche evolution along this key environmental gradient, the low frequency of these shifts, especially to calcium-poor soils, and the lesser time available for diversification in recently-derived lineages that have made these shifts, may ultimately be a key factor underlying the lower species richness of TDF plant communities on lower calcium soils. Notably, some lineages that have shifted to calcium-poor soils are relatively diverse in the study region and globally (e.g., Ericaceae: 12, ~3355 spp., respectively), but when compared to the summed diversity of the numerous lineages that have apparently retained an association with calcium-rich soils, the total diversity of calcium-poor sites is significantly lower.

The inferences drawn in this study to the ancestral niche of Basal Angiosperm and Eudicot taxa in TDF are significant for several reasons. First, the Basal Angiosperms represent a group or grade of taxa that are of great interest for understanding the early evolution of angiosperms (e.g., Feild et al. 2004; Soltis et al. 2005); while this group's contemporary diversity is not high, their evolutionary significance is considerable. A range of fossil and molecular evidence indicates that the angiosperms first evolved in the tropics during the Cretaceous and occurred in aquatic or mesic forest habitats; angiosperms did not colonize higher latitudes with frost or freezing temperatures for a considerable time (~ 20-30 my) after their initial appearance in the tropics (Behrensmeyer et al. 1993; Feild et al. 2004; Soltis et al. 2005; Fine & Ree 2006). While the results of this study situated in TDF at higher latitudes may be of limited relevance to the ecology of the earliest tropical Basal Angiosperms (e.g., Amborellaceae, Austrobaileyales; Feild et al. 2004), the later-diverging Basal Angiosperms represented in this study (e.g., taxa in Laurales, Magnoliales, Piperales) may provide some insight to the ecology of angiosperms that eventually colonized higher latitudes. To some extent, this study's findings on the calcium niche of these families suggest similarities to the 'dark and disturbed' model of Basal Angiosperm ecology developed in recent years (e.g., Feild et al. 2004; Feild & Arens 2005). Specifically, research on the ecology and ecophysiology of extant representatives of the earliest-diverging Basal Angiosperms indicates that early angiosperms may have occupied relatively dark, mesic forest habitats and exploited increased light levels following canopy disturbances to grow and reproduce (Feild et al. 2004; Feild & Arens 2005). In the present study, representatives of later-diverging Basal Angiosperm lineages in TDF appear to exhibit similar ecology, occupying mesic, nutrient-rich forests with relatively low understory light (e.g., under *Acer saccharum* canopies); in many cases, the reproduction and recruitment of these species also appears to be linked to canopy disturbance (Meier et al. 1995; Whigham 2004).

In contrast to the Basal Angiosperms, the Eudicots represent the great majority of angiosperm diversity extant today (~ 190,000 species or 75% of all angiosperms; Simpson 2006) and are the dominant members of vegetation in most terrestrial biomes around the world (e.g., except grasslands, boreal forest). Their explosive diversification in the late Cretaceous changed the face of terrestrial ecosystems (Behrensmeyer et al. 1992; Wang et al. 2009) and appears to have driven the subsequent diversification of many other plant and animal taxa (e.g., herbivorous beetles, ants, ferns; Farrell 1998; Moreau et al. 2006; Schuettpelz & Pryer 2009). In this study, early-diverging or Lower Eudicot species are strongly associated with calcium-rich soils. This suggests a general continuity with the ecology of Basal Angiosperms; however, it is the Lower Eudicots (e.g., Berberidaceae, Ranunculaceae) that are most frequently observed to attain high abundance and dominance in vegetation on calcium-rich sites. Further research on the ecological traits of the Lower Eudicots, and differences between these taxa and the Core Eudicots, may provide insight to key innovations or pre-adaptations that may have allowed this clade to diversify so extensively and become dominant in vegetation worldwide.

The results of this study also suggest that the Monocots may constitute a notable exception to the central role of calcium-rich soils in the early evolution of angiosperms in TDF. Recent phylogenetic analyses indicate that the Monocots diverged from a common ancestor shared by some taxa in the Basal Angiosperm grade, but not all (i.e., 'Basal Angiosperms' are a paraphyletic grouping; Davies et al. 2004). However, in this study, only taxa from Basal Angiosperm lineages that diverged subsequent to this split are present; as such, Monocots are sister to the remainder of the angiosperms included (Figure 4.7). My analyses reconstructed a moderate soil calcium niche for the common ancestor of the Monocots. In present-day TDF vegetation, monocots species are found across sites with a range of soil calcium conditions, with some notable genera having species present at both extremes (e.g., *Trillium undulatum* on acidic, calcium-poor soils and *T. grandiflorum* on circumneutral, calcium-rich soils; *Uvularia sessifolia* on calcium-poor soils and *U. grandiflora* on calcium-rich soils). More strikingly, some 'generalist' monocot species, such as *Maianthemum racemosum*, occur in vegetation across the full soil calcium gradient. As such, Monocot lineages show little evidence for phylogenetic niche conservatism relative to soil calcium conditions, but rather show signs of significant calcium niche lability or generalized tolerance.

Community Structure and Dominance: Evidence for Niche Pre-emption?

In addition to trends toward greater numbers of basally-derived and early-diverging taxa in TDF vegetation on calcium-rich soils, the analyses incorporating species' relative abundances also highlighted increased dominance by early-diverging angiosperm taxa on calcium-rich soils. In particular, a subset of Basal Angiosperm and Lower Eudicot species often comprised a substantial proportion of total herbaceous layer cover on calcium-rich sites (e.g., *Asarum canadense* in Aristolochiaceae, *Caulophyllum thalictroides* in Berberidaceae, *Actaea pachypoda* in Ranunculaceae). This pattern may be suggestive of niche pre-emption and incumbency among early-diverging angiosperm lineages. Specifically, fossil evidence suggests that representatives of early-diverging angiosperm taxa were present as minor components of Cretaceous period forests comprised predominantly of ferns and gymnosperms (e.g., conifers, cycads, ginkos; Behrensmeyer et al. 1992). With the rise and diversification of Core Eudicot lineages in the late Cretaceous, gymnosperm-dominated forests were rapidly replaced by angiosperm forests (Bond 1989; Behrensmeyer et al. 1992; Lupia et al. 1999; Wang et al. 2009). During this dramatic floristic turnover, it seems probable that angiosperm lineages already present and adapted to the understory of gymnosperm forests would have been ideally-situated to colonize and dominate the understories of newly-emerging angiosperm-dominated forest communities, especially on nutrient-rich sites well-suited to the ecophysiology of early angiosperms (Bond 1989; Feild et al. 2004; Coomes et al. 2005). Once occupying this niche, these lineages may have resisted displacement by later-evolving taxa. Consistent with the long-term occupation of these niches by Basal Angiosperms and Lower Eudicots, molecular and fossil evidence suggests that many of these early-diverging lineages were already represented by taxa comparable to extant species by the late Cretaceous or early Tertiary (e.g., *Paleoactaea* spp. and extant *Actaea* spp. in Ranunculaceae; Pigg & Devore 2005). The critical role of dynamics of this nature (e.g., pre-adaptation, niche preemption) in determining long-standing aspects of community structure and diversity are increasingly recognized in paleontological and neo-ecological studies (Brett et al. 1996; DiMichele et al. 2001; Ackerly 2004). While numerous, more recently-derived angiosperm lineages have continued to diversify and occupy calcium-rich soils, these lineages tend to exhibit lower abundance and have apparently not displaced the earlier-diverging angiosperm lineages that appear to have first occupied these types of habitats. As such, the results of the present study suggest that ecological dynamics that may have occurred in the forest understory during the late Cretaceous may still be an important driver of the community patterns evident in present-day TDF vegetation.

Notably, an interesting exception to the general trend toward dominance of calcium-rich soils by early-diverging lineages is suggested by the greater variability of AWPD scores on calcium-rich sites (Figure 4.6). Specifically, while many calcium-rich sites tend to show dominance by species from early-diverging lineages, some sites showed relatively high abundance of more recently-derived lineages. In particular, two 'types' of vegetation exhibited high AWPD scores despite having calcium-rich soils: plots with areas of water-saturated soil and plots with recent canopy disturbance. In the first case, plots containing ground-water seeps or wet coves often included vegetation dominated by species from more recently-derived lineages, such as *Laportea canadensis* (Urticaceae, 26 nodes to angiosperm root) or *Impatiens pallida* (Balsaminaceae, 18 nodes). In contrast, the Basal Angiosperm and Lower Eudicot species encountered in this study do not appear tolerant of water-saturated, anoxic soil conditions (J. Bellemare, *pers. obs.*). Consequently, this pattern may be suggestive of an open or empty niche on water-saturated soils that was relatively unoccupied by earlier-diverging angiosperms.

In the case of canopy disturbance on sites with high soil calcium levels, a range of more recently-derived angiosperm lineages appear to rapidly take advantage of high light and nutrient levels following disturbance. Disturbance-associated or 'gap-phase' species typical of this pattern include *Eupatorium rugosum* (Asteraceae, 27 nodes to root) and various *Rubus* spp. (Rosaceae, 22 nodes to root). While many Basal Angiosperm and Lower Eudicot taxa also respond positively to canopy disturbance with increased flowering and seed production (Meier et al. 1995; Whigham 2004), these taxa are often subsequently overtopped by plant species from more recently-derived lineages. In general, these gap-phase species tend to be taller in stature, exhibit less determinate growth, and appear to have higher relative growth rates than species from early-diverging angiosperm lineages (e.g., based on measures of Specific Leaf Area or SLA; J. Bellemare, *unpublished data*). Overall, these two types of exceptions to the lower AWPD scores of vegetation on calcium-rich soils seem suggestive of underexploited niches in a matrix habitat that is otherwise conducive to the dominance of early-diverging angiosperm lineages.

Insights to Phylogenetic Niche Conservatism

I have interpreted the results of this study to imply long-term phylogenetic niche conservatism among many angiosperm plant lineages associated with TDF. Indeed, the results appear to suggest that the ecological behavior of some Basal Angiosperms and Lower Eudicots, and the ecological structure of some TDF plant communities, may trace to the late Cretaceous period. While phylogenetic niche conservatism on this temporal scale (i.e., 10s of millions of years) may seem improbable given the evidence for rapid evolution in some plant lineages and the dramatic changes in the global environment during the Tertiary and Quaternary, several lines of evidence suggest that it may be plausible. First, while the TDF flora of the Northern Hemisphere has been severely impacted by climate change and glaciation during the Quaternary, there is generally little evidence for significant shifts or evolution in plant species' niches during this time; rather, most species appear to have either tracked their preferred niches through space (i.e., migration caused by niche conservatism) or become extinct (Huntley & Webb 1989; Svenning 2003). Second, at a greater temporal scale, many Basal Angiosperm and Lower Eudicot lineages exhibit disjunct distributions around the Northern Hemisphere tracing to the fragmentation of a more extensive mesophytic forest biome in the late Tertiary (Wen 1999; Donoghue & Smith 2004). Despite being separated for millions of years, many of these disjunct congeners still exhibit strikingly similar morphology and ecological behavior in TDF vegetation on opposite sides of the globe, highlighting the potential for long-term stasis in the traits and ecological niches of these lineages over millions of years (White 1983; Ricklefs & Latham 1992). Finally, at an even greater temporal scale, fossil evidence from the Tertiary suggests significant niche conservatism and morphological stasis among many angiosperm lineages associated with TDF (Crane et al. 1990; Pigg & DeVore 2005). Reporting on a survey of fossilized leaves from the early Tertiary (~ 65-60 mya), Crane et al. (1990) state: ‘the nearest living relatives of many extinct Paleocene plants are still associated in recent mixed mesophytic forest and this suggests that the climatic and, perhaps, edaphic tolerances of some individual angiosperm lineages have either remained more or less constant, or have exhibited similar patterns of change over the last 60 million years.’

While these various lines of evidence provide strong support for the possibility of long-term niche conservatism among early-diverging angiosperm lineages, the mechanisms of such a remarkable stasis in ecological traits remain to be determined. For example, some early-diverging lineages that seem to exhibit long-term niche conservatism in TDF have nonetheless undergone substantial radiations into other habitat types or biomes (e.g., Ranunculaceae in alpine or arctic habitats; Papaveraceae in open, disturbed habitats). This suggests that the niche conservatism evident for these lineages in TDF does not trace to intrinsic limits on adaptive change within these lineages (c.f., Bradshaw 1991). Rather, this might suggest a crucial role for the biotic community 'surrounding' these lineages in TDF in exerting stabilizing selection and maintaining long-term stasis in lineages' ecological behavior. However, that the effects of such biotic limitation could persist through long periods of community fragmentation, dissolution, and re-assembly during the Quaternary, when 'no modern analog' plant communities are widespread in the paleoecological record (Jackson et al. 2000), suggests that some degree of intrinsic limitation might be involved. Overall, the findings of this research and other studies suggest that much remains to be discovered regarding the ecological and evolutionary forces maintaining community structure over long periods of time (Brett et al. 1996; Miller 1996).

Conclusions

The results of this study provide compelling evidence that prominent gradients in plant species diversity and community structure in Temperate Deciduous Forests reflect the outcome of long-term, large-scale evolutionary processes. While contemporary environmental gradients clearly drive the distribution of plant diversity in this biome, the ultimate causes of variation in the number of angiosperm species associated with different environmental settings appear to be long-term trends toward niche conservatism among the angiosperms. In that the results also show evidence for dominance of the inferred 'ancestral niche' for angiosperms by early diverging lineages, the study likewise highlights the potential for ancient ecological dynamics (e.g., niche preemption) to have long-standing consequences for community structure. In conclusion, it is clear that in order to better understand the dynamics that influence the diversity and structure of communities, ecological theory will need to expand its temporal and spatial horizons to incorporate the types of long-term, large-scale processes that may ultimately underlie many prominent ecological patterns.

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