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Jesse Bellemare
Smith College, jbellema@smith.edu

David A. Moeller
University of Minnesota Twin Cities

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Climate Change and Forest Herbs of Temperate Deciduous Forests

Jesse Bellemare and David A. Moeller

Climate change is projected to be one of the top threats to biodiversity in coming decades (Thomas et al. 2004; Parmesan 2006). In the Temperate Deciduous Forest (TDF) biome, mounting climate change is expected to become an increasing and long-term threat to many forest plant species (Honnay et al. 2002; Skov and Svenning 2004; Van der Veken et al. 2007a), on par with major current threats to forest plant biodiversity, such as high rates of deer herbivory, intensive forestry, habitat fragmentation, and land use change (chapters 4, 14, 15, and 16, this volume). At the broadest scale, changing climate regimes are predicted to cause major shifts in the geographic distribution of the climate envelopes currently occupied by forest plants, with many species' ranges projected to shift northward or to higher elevations to track these changes (Iverson and Prasad 1998; Schwartz et al. 2006; Morin et al. 2008; McKenney et al. 2011). In parallel, these climate-driven range dynamics are likely to include population declines or regional extinctions for many plant species, particularly in more southerly areas and along species' warm-margin distribution limits (Iverson and Prasad 1998; Hampe and Petit 2005; Schwartz et al. 2006; Svenning and Skov 2006; Morin et al. 2008).

Among the plant species characteristic of TDF, forest herbs may be especially vulnerable to climate change for several reasons. First, many forest herbs have biological and ecological traits that may limit the rate at which they are capable of migrating in response to changing climate (e.g., species with seed dispersal mechanisms adapted primarily to local movement rather than long-distance dispersal; Van der Veken et al. 2007a). Second, the fragmentation and limited connectivity of forest areas due to agriculture, roads, and development in the modern landscape may exacerbate the innate challenges of long-distance dispersal and colonization for these species (Honnay et al. 2002; chapter 4 this volume). Finally, the geographic distributions of some forest herbs may still be impacted by past climate change (e.g., marginalization to southern areas by Pleistocene glaciations; Skov and Svenning 2004; Van der Veken et al. 2007a), making their rapid response to modern climate change less likely. Although the magnitude of the threat to forest herb biodiversity posed by climate change is not yet fully understood, several fields are providing important new insights into the relationship between temperate forest plants and climate change, including paleoecological (e.g., Williams et al. 2004) and phylogeographic research (e.g., Gonzales et al. 2008), comparative studies (e.g., Van der Veken et al. 2007a), and bioclimatic modeling approaches (e.g., Skov and Svenning 2004), as well as field-based experimentation (e.g., Van der Veken et al. 2007b; Warren et al. 2011). A synthetic view combining insights from these various fields will be key to understanding the challenges posed by modern climate change and developing effective conservation strategies for vulnerable plant species.

Although the rate and eventual magnitude of modern climate change are projected to differ qualitatively from climate dynamics in the recent geologic past (e.g., glacial cycles of the late Quaternary Period), important insights into the nature of threats to forest plant biodiversity and to the types of species most likely to be severely impacted by rapid climate change may be drawn from historical and biogeographic perspectives (Delcourt 2002; Svenning 2003; Van der Veken et al. 2007a; Petit et al. 2008; Willis et al. 2010). In this chapter, we review what is known about the long-term, large-scale range dynamics of forest herbs in response to past climate change and present a new biogeographic analysis investigating how contemporary distribution and diversity patterns among a subset of rare forest herbs may relate to these past climate dynamics. We also discuss how forest herb species may be affected by contemporary climate change and consider options for species conservation.

TEMPERATE DECIDUOUS FORESTS AND CLIMATE CHANGE: DEEP TIME PERSPECTIVES

The plant lineages that comprise the modern TDF biome have a deep and dynamic history in the Northern Hemisphere, inextricably linked to climate change over millions of years (Davis 1983; Donoghue and Smith 2004; Graham 2011). Almost all major temperate forest plant lineages have histories extending back 10s of millions of years into the Tertiary and upper Cretaceous periods, spanning climatic conditions that have been both significantly warmer and colder than at present (Graham 2011). For example, many of the angiosperm forest tree lineages that provide the structural foundation for modern TDF plant communities, including Aceraceae, Fagaceae, and Juglandaceae, trace their origins and rise to prominence to the upper Cretaceous (~ 100–65 million years ago; Manchester 1999; Willis and McElwain 2002; Wang et al. 2009). Similarly, characteristic forest herb lineages, such as the Aristolochiaceae, Berberidaceae, Ranunculaceae, and Liliaceae, emerged relatively early in the evolutionary diversification of angiosperms and include many genera that have apparently been closely associated with temperate forest habitats for millions of years since (i.e., phylogenetic niche conservatism; Ricklefs and Latham 1992; Wen 1999; Patterson and Givnish 2002).

During much of the upper Cretaceous and Tertiary, relatively warm and wet climatic conditions, combined with greater connectivity among landmasses in the Northern Hemisphere, allowed TDF-like vegetation to extend across large portions of North America and Eurasia, including many high latitude areas now occupied by boreal forest, tundra, and arctic desert (Manchester 1999; Wen 1999; Tiffney and Manchester 2001; Willis and McElwain 2002). With the onset of climatic cooling and drying in the Pliocene Epoch (~ 5.3–2.6 million years ago), and the advent of extensive continental glaciations in the Quaternary (~ 2.6 million years ago to present), the geographic distributions of TDF plant species were forced southward in a series of climate-driven range contractions during glacial maxima (Davis 1983; Latham and Ricklefs 1993; Delcourt 2002). Paleoecological studies, focused primarily on the pollen record from during and after the Last Glacial Maximum (LGM; ~ 21,500 years ago), have provided an important window on recent range dynamics, documenting large-scale shifts in the distributions of many forest plant species during periods of rapid climate change (Davis 1983; Prentice et al. 1991; Williams et al. 2004). Consistent with evolutionary research suggesting long-term niche conservatism in forest herbs (e.g., Ricklefs and Latham 1992; Wen 1999), these paleoecological studies tend to document migration or altitudinal shifts in response to past climate change, rather than substantial *in situ* evolution of species climatic tolerances (Huntley and Webb 1989; Martínez-Meyer and Peterson 2006; but see Davis et al. 2005).

Past climate change has also been linked to the extinction or regional extirpation of numerous TDF plant taxa (Davis 1983; Latham and Ricklefs 1993; Svenning 2003). Although relatively few plant extinctions are documented from the final glacial cycles of the Pleistocene Epoch (Bennett 1997; but see Jackson and Weng 1999), the initial shift to colder and drier climate in the Pliocene and the onset of extensive glaciations in the early Quaternary have been linked to the regional extinction of large numbers of characteristic TDF plant lineages in Europe, including *Carya*, *Hamamelis*, *Liriodendron*, *Magnolia*, *Tsuga*, and upward of 80 other woody plant genera (Davis 1983; Latham and Ricklefs 1993; Svenning 2003). Fewer forest plant extinctions are documented for eastern North America, but this period did see the regional extirpation of at least eight woody plant genera, including *Dendropanax*, *Platycarya*, *Pterocarya*, and *Sciadopitys* (Latham and Ricklefs 1993; Manchester 1999; Tiffney and Manchester 2001). In contrast, species from many of the plant 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 glaciations (Huntley 1993; Latham and Ricklefs 1993; Qian and Ricklefs 1999). Notably, the severe Pliocene and early Quaternary species losses in Europe appear to underlie 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 and Ricklefs 1993; Svenning 2003). These deep-time biogeographical patterns underscore the potential for long-lasting impacts of anthropogenic climate change on plant diversity and distribution in the TDF biome (Delcourt 2002; Thomas et al. 2004; Petit et al. 2008).

WHICH FOREST HERBS MAY BE MOST VULNERABLE TO CLIMATE CHANGE?

It is clear from past episodes of climate change and future projections that not all species are equally threatened by changing climate (Svenning 2003; Thomas et al. 2004; Thuiller et al. 2005; 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 are already adjusting their distributions in response to anthropogenic climate change (Parmesan and Yohe 2003; Hickling et al. 2005; Zuckerberg et al. 2009; Breed et al. 2012). Although similar range shifts in response to modern climate change have not yet been well documented for forest plants, the paleoecological record suggests that some species may be capable of relatively rapid range adjustments (e.g., Clark 1998; Williams et al. 2004). Nevertheless, the substantial numbers of forest plant extirpations and extinctions linked to the onset of a qualitatively new climatic regime during the late Tertiary and early Quaternary suggest that not all forest plants are equally resilient to abrupt climate change (Latham and Ricklefs 1993; Svenning 2003).

Of greatest concern in the face of modern climate change are species with limited geographic distributions, such as endemics and other small-ranged species (Thomas et al. 2004; Parmesan 2006; Schwartz et al. 2006; Thomas 2011). The increased risk of extinction projected for small-ranged species traces to a number of ecological and biogeographical factors. For example, macroecological studies have frequently detected a positive correlation between range size and local abundance, such that small-ranged species are often characterized by lower abundances and smaller population sizes than widespread species (Gaston 2003), a result that has been apparent in several plant-focused studies (Thompson et al. 1998; Murphy et al. 2006; Pocock et al. 2006). This characteristic, combined with the geographic clustering of populations, may expose small-ranged species to greater risk of extinction due simply to stochastic population processes or to chance regional events (e.g., drought, introduction of novel pathogens; Gaston 2003). In addition to risk factors that may be inherently linked to small range size, modern climate change poses a significant new threat to many small-ranged, endemic species (Thomas et al. 2004, 2011). Specifically, substantial geographic disjunctions are likely to develop between the locations of many small-ranged species' current ranges and the locations 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 at least some portions of these broadly distributed species' ranges are likely to remain climatically suitable into the future, buffering against climate-driven threats (Thomas et al. 2004; Schwartz et al. 2006). Without successful long-distance dispersal to track shifting climate zones as they move poleward, populations of small-ranged species may soon be exposed to novel climatic regimes that fall outside the range of climatic conditions they exist under currently; for some species this is likely to result in population declines or extinction (Thomas et al. 2004).

WHY MIGHT SMALL-RANGED SPECIES HAVE SMALL RANGES?

Ecologists have long recognized that the restricted distributions of small-ranged endemic plant species may be the outcome of a variety of causes (Willis 1922; Wherry 1944; Stebbins and Major 1965; Daubenmire 1978). Among potential drivers 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; Levin 2000; Lesica et al. 2006), or endemism due to the contraction of a formerly more extensive range (Daubenmire 1978). These three general classes of endemic species have been termed "ecological endemics," "neoendemics," and "paleoendemics," respectively (Stebbins and Major 1965; Daubenmire 1978; Estill and Cruzan 2001). In addition to these traditional explanations for the small ranges of endemic plant species, studies have increasingly raised the possibility that seed dispersal limitation may also be a factor contributing to the restricted geographic distributions of many small-ranged plants (Kropf et al. 2002; Rossetto and Kooyman 2005; Svenning and Skov 2007a; Van der Veken et al. 2007a; Rossetto et al. 2008). In the case of ecological endemics whose distributions are linked to unusual habitats (e.g., serpentine bedrock), suitable habitat patches are often widely scattered in a matrix of unsuitable habitat, likely making inter-site seed dispersal and range expansion difficult. For neoendemics, evidence suggests that some recently evolved species may simply have had limited time to disperse and expand their ranges (Lesica et al. 2006). Dispersal limitation has also been suggested as a key factor involved in the restricted distributions of some paleoendemics (Rossetto and Kooyman 2005; Rosetto et al. 2008). Although considerations of paleoendemics frequently focus on the dynamics of range fragmentation and decline leading to these species' restricted distributions (Daubenmire 1978; Levin 2000), it is also evident that the limited expansion of paleoendemics' ranges after conditions have ameliorated could be linked to dispersal limitation (Svenning and Skov 2007a; Van der Veken et al. 2007a; Hampe and Jump 2011). In general, the potential for dispersal limitation to be a key historical factor influencing the small range size of many endemic plants suggests that these species will have limited ability to track modern climate change.

Dispersal limitation of range size for endemic forest herbs could be traced to innate species characteristics, as well as aspects of regional landscape structure and biogeographic history. For example, studies have shown that factors such as low seed production, a lack of morphological adaptations for long-distance seed dispersal, and the absence of suitable dispersal agents may lead to significant dispersal limitation for many forest herbs (e.g., Matlack 1994; Bellemare et al. 2002; Verheyen et al. 2003; Van der Veken et al. 2007a; chapter 16, this volume). Although most studies investigating seed dispersal limitation in forest herbs have focused on local scales over relatively short timeframes (e.g., post-agricultural recolonization of secondary forests; Matlack 1994; chapter 16, this volume), evidence is increasing from studies at larger geographic scales that dispersal limitation may also contribute to limited range size in some forest herbs (e.g., Skov and Svenning 2004; Van der Veken et al. 2007a; Bellemare 2010). For example, Van der Veken et al. (2007a) found that European forest herbs with seeds adapted to local dispersal (e.g., via ants) and those lacking morphological adaptations for dispersal had significantly smaller geographic ranges than related species with seeds exhibiting adaptations for longer-distance dispersal (e.g., via wind or vertebrates). These studies have highlighted the potential for key climate change risk factors, like small range size and dispersal limitation (Thomas et al. 2004), to be causally linked in forest herbs (Van der Veken et al. 2007a).

WHERE ARE SMALL-RANGED FOREST HERBS IN EASTERN NORTH AMERICA?

Given that small-ranged species are expected to be at increased risk from climate change, what do we know about the current distributions of small-ranged forest herbs in eastern North America? To date, there have been no comprehensive reviews of the distribution of small-ranged forest plants (i.e., endemics) or analyses of patterns of endemism focused specifically on the TDF biome. Prior studies by Stein et al. (2000) and Estill and Cruzan (2001) have surveyed patterns of endemism in portions of eastern North America, but neither focused on forest habitats in detail. These investigations highlighted numerous "hotspots" of endemism in non-forest habitats (e.g., scrub and sand hill vegetation in central Florida, open cedar glade habitats in central Tennessee), in addition to a limited number of hotspots in TDF (e.g., the southern Appalachian Mountains; Estill and Cruzan 2001). Although these earlier studies have been key to mapping the distribution and diversity of plant endemics in general, a biome-centered survey focusing specifically on small-ranged plants associated with TDF has not been conducted. Such a study will be crucial in the context of climate change, as the unique ecology and biogeographic history of forest plants may predispose them to climate-related vulnerabilities. Further, conservation options for small-ranged forest plants may include some approaches (e.g., assisted colonization) that may be less feasible for species associated with other, more unusual and spatially limited habitats where endemics are often found, such as serpentine barrens or limestone glades.

In the analysis presented here, we have focused specifically on the distribution of small-ranged forest herbs associated with TDF habitats in eastern North America. To identify appropriate species for inclusion in this survey, we visually inspected all plant species distribution maps developed by the Biota of North America Program (BONAP; Kartesz 2010) for species with geographic ranges centered in eastern North America. These maps are available online (www.bonap.org) and are updated on a continuing basis as new records become available; the distribution maps used in the present analysis were accessed from BONAP in 2010. For the purposes of this survey, we defined "small-ranged" plant species as those with distributions including 70 or fewer U.S. counties. Although many plant species with small ranges are classified as endangered or threatened at the federal or state level, our species selection process did not consider current listed status as a criterion; rather, we consider range size as an important correlate of future risk in the face of climate change, regardless of species' current legal status (cf. Harris and Pimm 2008; also see chapter 4, this volume, for a review of population biology and threats to federally listed forest herbs).

For each small-ranged herbaceous species with a distribution centered in eastern North America, we reviewed habitat information to identify those that were associated with deciduous forest habitats using the *Flora of North America* (Flora of North America editorial committee 1993+) and key regional references (e.g., Radford et al. 1968; Gleason and Cronquist 1991; Yatskievych 1999; Wunderlin and Hansen 2003; Weakley 2011). Species were selected for inclusion if their habitat descriptions included deciduous forest or woodland, or mixed deciduous-coniferous forest (e.g., hardwood-hemlock or oak-pine forest). Species were also included if their habitat was more specialized but still typically situated within a deciduous forest matrix (e.g., shaded ledges, woodland clearings, forest edges, forested seeps and stream banks). A subset of the forest herb species included was also described as occasionally occurring outside forest habitats in meadows, open rocky areas, wetlands, or along roadsides. Of note, BONAP distribution data for plant species in Canada are provided at a coarser scale (i.e., province level) than within the U.S. (county level); however, this did not become a significant issue in quantifying species distributions as almost all forest herbs with small ranges were distributed substantially south of the Canadian border.

In total, the criteria outlined above resulted in a set of 189 small-ranged forest herb species native to deciduous forests in eastern North America (appendix 21.1). These species represent taxa from 38 families and 87 genera, with four of these families accounting for ~ 50 percent of the species included: Asteraceae (34 spp., ~ 18 percent), Lamiaceae (21 spp., ~ 11 percent), Melanthiaceae (21 spp., ~ 11 percent), and Cyperaceae (20 spp., ~ 11 percent). Notably, representatives of the latter two were drawn almost entirely from *Trillium* and *Carex*, with 21 and 18 small-ranged forest species, respectively. Pteridophytes and lycophytes contributed only two small-ranged species to the final analysis (*Botrychium mormo* W. H. Wagner and *Gymnocarpium appalachianum* Pryer), as most ferns and lycophytes associated with forest habitats in eastern North America are relatively widespread.

To provide quantitative estimates of range size and geographic position for the 189 small-ranged forest herbs, the BONAP county-level distribution maps were digitized into a geographic information system (GIS). The total range area occupied by each species was calculated as the summation of the areas of all the counties occupied by that species; additionally, a centroid was estimated for each range based on these county-level distributions. Range sizes exhibited a positively skewed distribution, with a median range size of ~ 61,448 km^2 (fig. 21.1). Minimum range size was ~ 1,600 km^2 for *Onosmodium decipiens* J. Allison, a narrow endemic native to open woodland and glade habitats on dolomite bedrock in Bibb County, Alabama. Maximum range size was ~ 280,000 km^2 for the relatively more widespread *Meehania cordata* (Nutt.) Britton, a species native to mountain woods in the mid-Appalachians from western North Carolina to southwestern Pennsylvania. Notably, even the range sizes of the most widespread small-ranged species included in our analysis, such as *M. cordata*, are still almost an order of magnitude smaller than the ranges of large-ranged forest herbs like *Podophyllum peltatum* L., *Asarum canadense* L., or *Sanguinaria canadensis* L. (estimated range areas ~ 2.3, 2.7, and 3.5 million km^2, respectively).

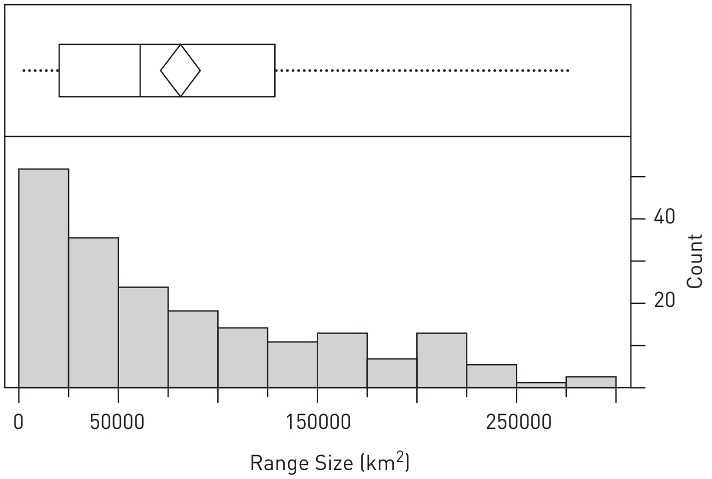

FIGURE 21.1 Range sizes of the 189 small-ranged forest herb species included in this study. Range sizes were estimated as the total area of U.S. counties occupied by each species, as determined from Biota of North America Program (BONAP) county-level species distribution maps accessed in 2010. Box plot (top) depicts mean range size (diamond), median range size (vertical line), the 25th and 75th quantiles (outer edges of box), and dashed "whisker" lines mark the range of data beyond these quantiles.

To assess overall patterns of small-ranged forest herb distribution and diversity in eastern North America, range maps for the 189 species were compiled in a GIS to create a map of small-ranged species richness (no. of small-ranged species per county). The results of this analysis show that the distribution and diversity of small-ranged forest herbs across eastern North America exhibit marked biogeographical patterning, with both pronounced hotspots and coldspots of endemic species richness (fig. 21.2). At the broadest scale, small-ranged forest herbs are relatively common in the southeastern U.S. and lower Midwest, but are almost entirely absent from TDF areas north of the Last Glacial Maximum (LGM) in the Northeast, upper Midwest, and adjacent Canada (figs. 21.2 and 21.3). Although these northern areas often include well-developed forest herb communities, almost all of the species found north of the LGM have relatively large geographic ranges when compared to the small-ranged forest herb species that were the focus of this analysis.

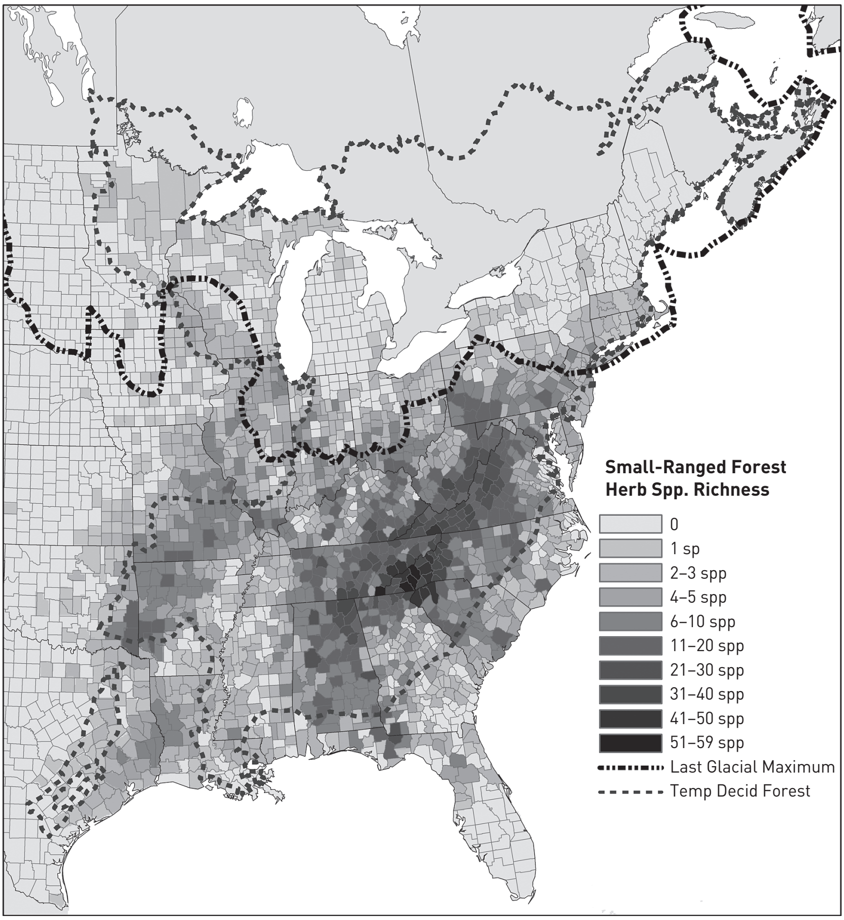

FIGURE 21.2 Distribution and richness of 189 small-ranged forest herb species in eastern North America relative to the distribution of the Temperate Deciduous Forest biome (TDF; green line) and the Last Glacial Maximum (LGM; blue line). County-level richness of small-ranged forest herbs ranges from a high of 59 species in western North Carolina to a low of zero species recorded across much of the formerly glaciated northern portion of the TDF biome, and some counties in the southeastern U.S. along the Coastal Plain and Mississippi Embayment. Boundaries of TDF biome follow Ricketts et al. (1999); the LGM boundary was derived from state-level surficial geology maps.

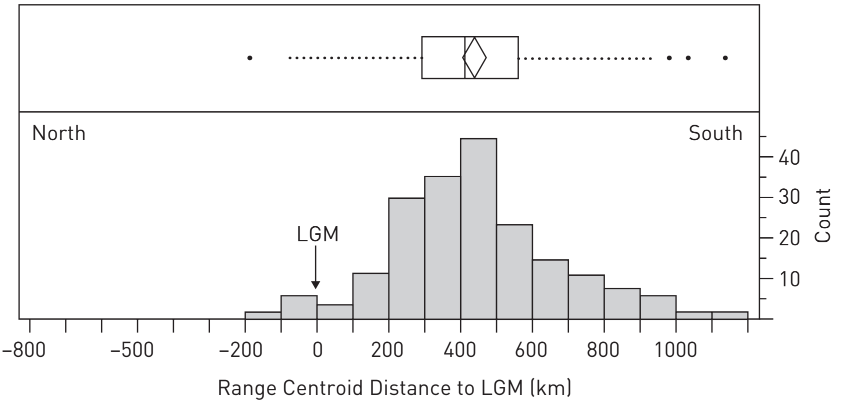

FIGURE 21.3 Range centroid distances to the LGM boundary for 189 small-ranged forest herb species in eastern North America. Positive values indicate range centroids that are situated south of the LGM, outside formerly glaciated regions; negative values indicate centroids located north of the LGM, within formerly glaciated regions; the LGM boundary is set to 0 on the distance axis. The mean distance from range centroids north to the LGM was 438 km (± 224 SD). The distance axis extends to –800 km, or 800 km north of the LGM, as the TDF biome extends northward into areas of Canada ~ 800–900 km north of the LGM; however, no small-ranged species centroids are located further than 186 km north of the LGM (i.e., –186 km on *x* axis in this figure). In contrast, the centroids of 16 small-ranged forest herb species are found near or beyond the southern boundaries of the TDF biome in the southeastern U.S., ~ 800–1,200 km south of the LGM.

Among the 189 species included in this analysis, almost all (183 spp., ~ 97 percent) have range centroids situated substantially south of the LGM (mean distance: 438 km ± 224 SD; fig. 21.3). Of the six species with range centroids falling north of the LGM boundary, only *Botrychium mormo* (a pteridophyte native to sugar maple forests in northern Minnesota, Wisconsin, and Michigan) has a range situated substantially north of the LGM (centroid located 186 km inside LGM boundary); the remaining five species have ranges that straddle the LGM boundary (centroids < 100 km inside LGM; fig. 21.3). This pattern of low richness of endemic forest herbs in formerly glaciated regions emerged despite the large spatial extent of the TDF biome in areas north of the LGM. In fact, portions of the TDF biome extend 800–900 km north of the LGM into Canada, but no small-ranged species distributions approached this limit. In contrast, some areas along the southern margins of the TDF biome, lying 800–1,200 km south of the LGM, have high concentrations of small-ranged forest herb species (fig. 21.2). Indeed, 16 of the small-ranged species (~ 8 percent) included in this analysis have range centroids located on or outside of the southern boundary of the TDF biome; these outlying species tend to be associated with patches of TDF-like habitat in cooler and more mesic sites on the coastal plain in the southeastern U.S., such as north-facing slopes or bluffs along rivers.

In contrast to the general absence of small-ranged forest herbs from most northern portions of the TDF biome, the southeastern U.S. and lower Midwest include several geographically distinctive hotspots of small-ranged forest herb diversity, as well as a more heterogeneous background pattern of low to moderate levels of endemism across much of the region (fig. 21.2). Although the criteria for defining and delineating hotspots can be somewhat subjective when confronted with the complex diversity patterns evident in our results, we focus here on three prominent areas that stand out due to their geographic distinctiveness and relatively high diversity of small-ranged forest herbs: the *Southern Appalachians*, the *Apalachicola River* region in the Florida panhandle and adjacent Georgia, and the *Interior Highlands* of Arkansas and Missouri (fig. 21.2).

The Southern Appalachian Hotspot

Previous studies have highlighted the southern Appalachian Mountains as a major center of plant diversity and endemism in eastern North America (e.g., Stein et al. 2000; Estill and Cruzan 2001). This trend clearly holds for small-ranged forest herbs, with counties in western North Carolina, eastern Tennessee, southwestern Virginia, and extreme northern Georgia and western South Carolina including the highest richness of small-ranged forest herbs anywhere in eastern North America (peaking at 59 species with overlapping distributions in western North Carolina; fig. 21.2). In total, 119 of the 189 small-ranged species (63 percent) reviewed in this survey have distributions that overlap the Southern Appalachian hotspot; among these 119 species, 18 have ranges that are entirely restricted to this region (i.e., 15 percent of the species occurring in the hotspot). For example, *Diphylleia cymosa* Michx. is found only in cool, mesic forests at high elevations in the southern Appalachian Mountains, while *Shortia galacifolia* Torr. & A. Gray is a well-known narrow endemic native to just six counties in the region (Weakley 2011). The spatial extent of this hotspot also seems remarkable: Beyond the core area of high diversity and endemism in the southern Appalachian Mountains of western North Carolina, a broader zone of high diversity extends along most of the mid- to southern Appalachian Mountains, from West Virginia and western Virginia, south to the southern edges of the Appalachian Plateau in northeastern Alabama (fig. 21.2).

The Apalachicola River Hotspot

The Apalachicola River area of the Florida panhandle and adjacent southeastern Alabama and southwestern Georgia is the region with the next highest richness of small-ranged forest herbs, peaking at 21 species with overlapping distributions in both Gadsden County, Florida, and Decatur County, Georgia. Overall, 29 small-ranged forest herb species have distributions that include counties in and around the Apalachicola River area. Importantly though, this hotspot is comprised primarily of species for which the Apalachicola River area represents a southernmost extension or disjunct station in geographic ranges that also include counties farther to the north in central Alabama, the southern Appalachian Mountains, or the adjacent Piedmont. Of the 29 small-ranged forest herbs in this area, only two (7 percent) are narrow endemics restricted entirely to the Apalachicola River hotspot (*Carex thornei* Naczi and *Liatris gholsonii* L. C. Anderson); one additional species, *Matelea alabamensis* (Vail) Woodson, occurs in this area, as well as in one county in eastern Georgia. Notably though, the Apalachicola River hotspot does also include several narrow endemics in its woody flora, such as *Magnolia ashei* Weatherby, *Taxus floridana* Nuttall ex Chapman, and *Torreya taxifolia* Arnott.

The Interior Highlands Hotspot

The Interior Highlands hotspot, including parts of the Ouachita Mountains and Ozark Plateau in Arkansas, Missouri, and extreme eastern Oklahoma, has received considerably less attention in the botanical and ecological literature on forest plant diversity than areas further to the east; however, it stands out in this analysis as a key hotspot of small-ranged forest herb diversity, with 28 species co-occurring in the region. Although characterized by a slightly lower peak of small-ranged forest herb richness (19 species in Montgomery County, Arkansas) than the Apalachicola River hotspot, it is nonetheless a distinct and important area. First, it is geographically and physiographically isolated from the other major hotspots of forest herb diversity in eastern North America. Second, narrow endemics comprise a substantially larger component of the regional flora than in the other two hotspot regions: Seven of the 28 small-ranged species (25 percent) associated with the Interior Highlands hotspot are narrow endemics restricted to just this region. These include species such as *Carex latebracteata* Waterfall, *Delphinium newtonianum* D. M. Moore, and *Solidago ouachitensis* C. E. S. Taylor & R. J. Taylor, as well as recently described forest herb species such as *Hydrophyllum brownei* Kral & V. M. Bates (Kral and Bates 1991), *Polymnia cossatotensis* Pittman & V. M. Bates (Pittman and Bates 1989), and *Stachys iltisii* J. Nelson (Nelson 2008).

Secondary Hotspots

In addition to the three geographically distinctive hotspots described above, a number of secondary hotspots with lower peaks of diversity (e.g., 10–15 overlapping distributions) are also apparent in other parts of the southeastern U.S. and lower Midwest. Among these, an area around Tuscaloosa County in central-western Alabama emerges as a hotspot for regional and local endemics that is distinct from the Southern Appalachian hotspot to the northeast. Further to the east, in the Piedmont region, several South Carolina counties along the upper Savannah River watershed also exhibit relatively high densities of small-ranged forest herbs, including some narrow endemics, like *Trillium discolor* Wray ex Hook. and *T. persistens* Duncan. Further to the north, a number of small-ranged forest herb species have ranges centered along the Ohio River Valley in southern Ohio, Indiana, Illinois, and adjacent northern Kentucky (e.g., *Oxalis illinoiensis* Schwegm., *Penstemon deamii* Pennell). Finally, two coastal plain counties, Pender County, North Carolina, and Berkeley County, South Carolina, also stand out as areas with relatively high numbers of small-ranged forest herbs.

Trends in Range Size

In addition to overall patterns in the distribution and diversity of small-ranged forest herbs, we also analyzed correlations between range size and three geographical and historical factors: range centroid longitude, centroid latitude, and centroid distance to the LGM boundary. Among the 189 species, no trend in range size relative to longitude was apparent, despite expectations that decreased rainfall and water availability to the west in our study area might influence range size for forest herbs (fig. 21.4a, $p > 0.05$). In contrast, a highly significant positive correlation was apparent between range size and latitude (fig. 21.4b; $F_{1,187} = 11.5$, $p = 0.0009$, $R^2 = 0.06$). This correlation is consistent with the commonly observed biogeographic trend of increasing range size with increasing latitude, often referred to as Rapoport's Rule (Lomolino et al. 2006). Although a number of hypotheses have been advanced to explain this pattern (e.g., increases in species niche breadths with latitude; Stevens 1989), the relatively

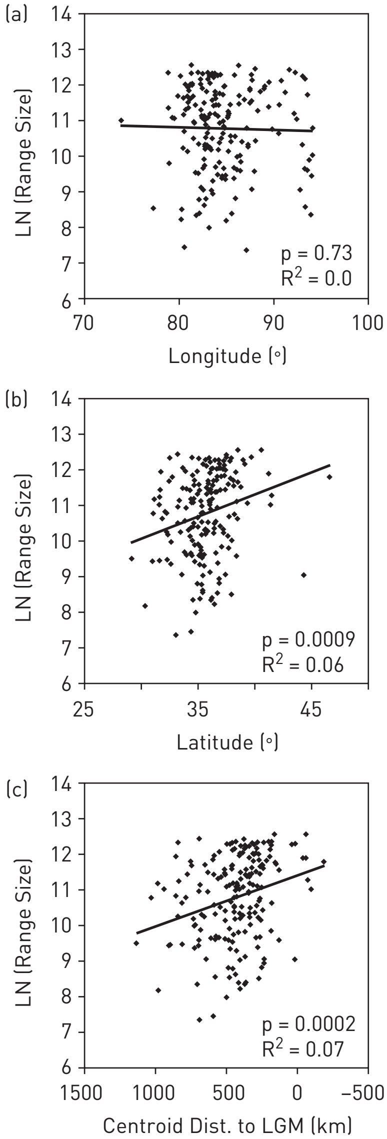

FIGURE 21.4 Correlations between natural log-transformed range size and species' range centroid longitude (panel A), latitude (B), and distance to the LGM boundary (C) for 189 small-ranged forest herbs in eastern North America. Among the small-ranged forest herbs included in this study, range size varied from ~ 1,600 km^2 to ~ 280,000 km^2. The *p*-values and R^2 indicated in each panel are derived from simple linear regression; the associated F statistics are as follows: $F_{1,187}$ = 0.1 for panel A; 11.5 for B; 14.0 for C.

abrupt truncation in the distribution and richness of small-ranged species near the LGM boundary, rather than a more continuous decline tracking latitude north of the LGM, suggests an important historical component to the pattern in our study area (cf. Cowling and Samways 1994; Dynesius and Jansson 2000; Jansson 2003). Consistent with this possibility, the trend in range size is fit more closely by a regression in range centroid distance to the LGM boundary ($F_{1,187}$ = 14.0, p = 0.0002, R^2 = 0.07; fig. 21.4c), an analysis that takes into account the irregular border and major southward lobes of the last glacial advance (fig. 21.2). Overall, these results show that the range sizes of small-ranged forest herbs tend to increase toward the LGM, even while very few of these species have distributions that actually extend north of this boundary.

FROM PATTERN TO PROCESS: INSIGHTS INTO THREATS POSED BY MODERN CLIMATE CHANGE

The absence of small-ranged forest herbs from most formerly glaciated portions of eastern North America is consistent with observations on patterns of endemism in other areas of the Northern Hemisphere and suggests that past climate change and glaciation have had a major effect on the distributions of endemic species (Cowling and Samways 1994; Dynesius and Jansson 2000; Jansson 2003; Finnie et al. 2007; Sandel et al. 2011). Similarly, the concentration of many small-ranged species in distinct hotspots of endemism far to the south of the LGM, as seen in the results of this survey, has frequently been taken as indirect evidence for the locations of Pleistocene-era glacial refugia (Estill and Cruzan 2001; Médail and Diadema 2009). Such hotspots are thought to have developed when the ranges of temperate zone species contracted south to small areas of suitable habitat during the LGM (Estill and Cruzan 2001; Svenning and Skov 2007a). With the amelioration of climate in the late Pleistocene and early Holocene eras, the distributions of many temperate plant species expanded out of these southern areas (Davis 1983; Prentice et al. 1991; Cain et al. 1998; Williams et al. 2004), but the ranges of a subset of forest plant species appear to have remained restricted to regions in or around these former glacial refugia (Svenning and Skov 2007a).

All three of the major hotspots identified in this study correspond to areas previously suggested as important Pleistocene-era refugia in eastern North America. For example, the Apalachicola River area has long been hypothesized as a glacial refugium (Thorne 1949; Estill and Cruzan 2001). Similarly, increasing population genetic evidence points to the southern Appalachian Mountains as an area where populations of some temperate forest plant species may have persisted during the LGM (McLachlan et al. 2005; Gonzales et al. 2008). The Interior Highlands hotspot identified in this study has also been described as a Pleistocene-era refugium (Ricketts et al. 1999), although most recent research has focused on biogeographic and phylogeographic evidence from animal species native to the region (e.g., Carlton and Robison 1998; Near et al. 2001). One notable exception to this pattern of correspondence between putative glacial refugia and small-ranged forest herb diversity hotspots is seen in the Lower Mississippi River Valley: This region has frequently been mentioned as a likely refugium for temperate forest species (e.g., Delcourt and Delcourt 1975; Cain et al. 1998; Jackson et al. 2000), but exhibits low diversity of small-ranged forest herbs (fig. 21.2).

It is also clear from the results of this study that not all small-ranged forest herbs are restricted exclusively to the limited number of hotspots described above. Indeed, the low-to-moderate levels of small-ranged forest herb diversity apparent across much of the southeastern U.S. and lower Midwest are surprising, particularly when contrasted to the absence of small-ranged forest herbs from most areas north of the LGM (figs. 21.2 and 21.3). This pattern may be suggestive of several interesting processes bearing on post-glacial migration rates and so-called cryptic refugia. First, at the broadest geographic scale, it is apparent that very few small-ranged forest herbs have substantially expanded or shifted their distributions into formerly glaciated regions in the north; only six of the 189 species (3 percent) included in this analysis had range centroids situated north of the LGM, and most species range centroids were situated substantially south of this boundary (mean distance to LGM = 438 km; fig. 21.3). This pattern emerges despite nearly ~ 15,000 years since widespread deglaciation and seems to stand in marked contrast to the relatively rapid northward range expansion inferred for other temperate forest plant species (e.g., Cain et al. 1998; Clark 1998; Williams et al. 2004).

In particular, the dispersal and range dynamics suggested by the results of the present survey appear to diverge most strikingly from conclusions drawn by Cain et al. (1998) regarding forest herb migration in response to climate change. Cain et al. (1998) reviewed literature on the dispersal ability of 28 forest herbs and highlighted the mismatch between the limited seed dispersal distances reported in the field for these species and the substantial distances many must have migrated during the Holocene to reach current range boundaries in the north. Based on these discrepancies, Cain et al. (1998) concluded that rare long-distance dispersal events likely enable rapid migration and range shifts in forest herbs (cf. Clark 1998), even for species that otherwise appear to be severely dispersal-limited based on field observations (e.g., Matlack 1994). Notably though, almost all of the forest herbs considered by Cain et al. (1998) were common large-ranged species with distributions extending well into formerly glaciated regions (e.g., *Asarum canadense*, *Sanguinaria canadensis*, *Geranium maculatum* L.). Rare long-distance dispersal events clearly need to be invoked to account for the distribution patterns seen among these wide-ranging species, and subsequent studies have documented potential mechanisms (e.g., *Trillium* seeds dispersed by deer; Vellend et al. 2003). However, in contrast to the species considered by Cain et al. (1998), the present study focused on small-ranged endemics, a group that has typically been overlooked in the plant dispersal and paleoecological literature, even though it is among such species where long-term dispersal limitation of range size is a reasonable hypothesis (Skov and Svenning 2004; Van der Veken et al. 2007a).

Prior studies have linked small range size in forest herbs to biological and ecological traits like limited seed production and dispersal ability (Van der Veken et al. 2007a). We have not formally reviewed the life history traits of the 189 species included in the present study, as little published data is available on these relatively rare, range-restricted species. However, it is striking that a large number of these forest herbs come from families or genera known to include species with limited dispersal ability (e.g., species with ant-dispersed seed or no obvious mechanism of dispersal: *Carex* spp., *Hexastylis* spp., *Trillium* spp., various Lamiaceae and Ranunculaceae spp.). Similarly, the presence of only two ferns and lycophytes (i.e., taxa that typically produce large quantities of wind-dispersed spores) in the set of small-ranged species identified for the analysis seems telling. In contrast, the large number of small-ranged Asteraceae (34 spp.), a family often characterized by wind-dispersed propagules, was surprising. Clearly, further research on the trait characteristics of these small-ranged species is needed, especially in a comparative phylogenetic context including wide-ranging congeners or confamilials (cf. Lavergne et al. 2004; Van der Veken et al. 2007a).

The second pattern evident in our results with implications for estimating migration capacity of forest herbs was the close proximity of some small-ranged species distributions to the LGM boundary. Specifically, 43 of the small-ranged forest herbs (23 percent of total) had range centroids ≤ 300 km from the LGM, well outside the major hotspots identified in the southeastern U.S. (fig. 21.3). This pattern may suggest that the geographic ranges of this subset of species have shifted or expanded substantially northward during the Holocene Epoch, a dynamic that would be consistent with the larger range size exhibited by species distributed closer to the LGM (fig. 21.4). However, this finding may also indicate that some small-ranged forest herbs persisted through the LGM in cryptic northern refugia, outside the areas traditionally cited as major glacial refugia in the southeastern U.S. (e.g., the Gulf Coast and the lower Mississippi River Valley; Delcourt and Delcourt 1975, 1987; Davis 1983).

Increasing genetic evidence points to the existence of such cryptic northern refugia during the LGM, as recent phylogeographic studies have documented unique haplotypes in temperate forest plant populations well to the north of the Gulf Coast and the lower Mississippi River Valley (McLachlan et al. 2005; Hu et al. 2009). These divergent genetic lineages are believed to represent the descendants of populations that were isolated in distinct glacial refugia during the LGM or earlier glacial maxima (Gonzales et al. 2008). For example, Gonzales et al. (2008) documented *Trillium cuneatum* Raf. haplotypes in areas of Kentucky and Tennessee, as well as in the southern Appalachians, that were divergent relative to those seen farther south in the species' range. Similar associations between unique haplotypes and the southern Appalachian Mountains have been detected for *Acer rubrum* L. and *Fagus grandifolia* Ehrh. (McLachlan et al. 2005). More strikingly, Beatty and Provan (2011) presented genetic evidence of a glacial refugium for *Monotropa hypopitys* L. in the unglaciated "Driftless Area" of southwestern Wisconsin and southeastern Minnesota, a region that also emerged in our analysis as a northern area with a relatively high richness of small-ranged forest herbs (fig. 21.2).

The northern refugia inferred from these genetic data are referred to as "cryptic" in that paleoecological studies focused on the pollen record have generally not detected the presence of TDF plant species in these areas during the LGM, likely due to small population sizes, low density, and isolation (McLachlan et al. 2005; Beatty and Provan 2011). Regardless, most forest herbs are missing from the pollen record because they produce only limited quantities of insect-dispersed pollen, as compared to the more abundant wind-dispersed pollen of many trees, grasses, and sedges. As such, prior to these recent genetic studies, forest herbs have largely been invisible to paleoecological studies based on the pollen record, and their range dynamics were typically extrapolated from those of better-documented TDF tree species (e.g., Cain et al. 1998).

The new evidence for cryptic northern refugia during the LGM may have significant implications for estimates of post-glacial migration rates (McLachlan et al. 2005). Specifically, the persistence of temperate forest plant populations within a few 100 km of the LGM boundary would imply that post-glacial migration rates may have been substantially lower than what has previously been inferred based on models assuming long-distance dispersal from the Gulf Coast or lower Mississippi River Valley (e.g., Cain et al. 1998; Clark 1998; see also MacLachlan et al. 2005). As such, the high migration potential originally estimated for many forest plant species based on the pollen record is now being reevaluated, with critical implications for how rapidly species can be expected to migrate in response to modern climate change (McLachlan et al. 2005). Indeed, some studies have projected that plant migration rates will need to approach 1,000 m/yr or more to keep pace with modern climate change, but even the fastest migrations of the late Pleistocene and early Holocene now appear to have been on the order of 100 m/year or less (McLachlan et al. 2005; Petit et al. 2008).

CONSERVATION IMPLICATIONS

Although the co-occurrence of many small-ranged forest herbs in regional hotspots in the southeastern U.S. would likely facilitate conservation planning under more stable climatic conditions, the rapid climate change projected for coming decades may substantially complicate this goal. In particular, because hotspots of endemism and diversity tend to be localized to southern areas where TDF species survived climatic *cooling* in the past, their ranges may now be poorly positioned to withstand future climatic *warming* (Delcourt 2002; Hampe and Petit 2005; Wilson et al. 2005; Ashcroft 2010). Consistent with this prediction, relict populations of a number of boreal and TDF plant species already exhibit limited or failing recruitment at their southern range edges in Europe (e.g., García et al. 1999; Hampe and Arroyo 2002; Mejías et al. 2002, 2007; Castro et al. 2004; Beatty et al. 2008). In eastern North America, few studies have focused on the population dynamics of small-ranged forest plants at the southern margins of the TDF biome, but some researchers have suggested that the severe decline of one narrow endemic, *Torreya taxifolia*, native to the Apalachicola River hotspot, may be linked in part to climate change (Barlow and Martin 2004; Schwartz 2004).

Interestingly, there is evidence that hotspots of endemism tend to occur in areas that have historically permitted some resilience to climate change (Jansson 2003; Ashcroft 2010; Sandel et al. 2011). For example, regions with substantial topographic heterogeneity may allow species to survive via local elevational shifts rather than large-scale migration; similarly, the presence of microhabitats that may moderate climatic stress, such as mesic sites, river valleys, and north-facing slopes, may allow for local persistence despite changing climate (Jansson 2003; Ashcroft 2010; Sandel et al. 2011). Consequently, it is possible that the hotspots and small-ranged species identified in this analysis may be associated with areas that exhibit some resilience to near-term climate change; however, the magnitude of modern climate change may eventually overwhelm such environmental buffering. In this context, small-ranged forest herbs native to areas with limited topographic heterogeneity (e.g., Gulf Coastal Plain, portions of midwestern U.S.) may be at increased risk relative to those in mountainous areas, as successful tracking of climate envelopes for the former species will likely require larger latitudinal displacement of ranges (cf. Sandel et al. 2011). At the other extreme, small-ranged species linked to high elevation habitats in the southern Appalachian Mountains may also face severe habitat loss due to upward elevational shifts in regional climate zones, with the potential for some habitats to disappear entirely off the tops of southern mountains (i.e., the so-called escalator effect; see also Delcourt and Delcourt 1998).

In the face of such climate-driven threats, conservationists have traditionally stressed the importance of habitat corridors and landscape connectivity to facilitate natural dispersal and range shifts (Hunter et al. 1988; Hannah et al. 2002; Hunter 2007). Unfortunately, this approach may prove ineffectual for species that are severely dispersal-limited, or for those whose present ranges and potential future habitat are separated by large expanses of unsuitable habitat (Thomas et al. 2004; Thomas 2011; chapter 4, this volume). Given these challenges, some researchers have begun to consider the potential for assisted colonization or managed relocation to avoid species extinctions due to rapid climate change (Barlow and Martin 2004; McLachlan et al. 2007; Hoegh-Guldberg et al. 2008; Thomas 2011). Assisted colonization proposes intentionally translocating species to regions where they have not occurred historically, but where they are expected to survive as self-sustaining, naturalized populations as climate changes in the future (McLachlan et al. 2007; Hoegh-Guldberg et al. 2008; Thomas 2011). This unconventional approach to ex situ conservation may be necessary for the long-term preservation of some species, as reintroduction into climatically compromised former ranges may be impossible, and the indefinite maintenance of species (and the genetic diversity within them) in botanic gardens and arboreta may be impractical (MacLachlan et al. 2007; Oldfield 2009; Thomas 2011). Long-term seed storage in seed banks (e.g., via cryopreservation) also offers some potential to preserve rare and climate-threatened species (Li and Pritchard 2009), but using this technique alone might consign species to extinction in the wild and reduce the potential for future adaptive evolution in response to climate change (Davis et al. 2005).

Nevertheless, the possibility of assisted colonization has sparked vigorous debate among ecologists and conservationists, particularly regarding the potential for invasiveness among translocated species (e.g., Mueller and Hellmann 2008; Ricciardi and Simberloff 2009; Minteer and Collins 2010). However, to date, most discussions of assisted colonization have been largely hypothetical in nature or illustrated with a range of extreme examples drawn from around the globe; as such, these discussions have tended to lack clear grounding in the ecology, biogeographic history, and likely candidate species of any particular region or biome. In the final sections of this chapter, we discuss assisted colonization as a potential conservation tool for small-ranged forest herbs that may be threatened by modern climate change.

WOULD ASSISTED COLONIZATION OF SMALL-RANGED FOREST HERBS BE FEASIBLE?

Even if evidence indicated the climate-driven decline of a small-ranged forest herb, what is the likelihood that self-sustaining populations of such a species could be successfully established beyond its current range boundaries? Most species distribution models in ecology, biogeography, and paleoecology are premised on the assumption that contemporary range edges represent a dynamic equilibrium between environmental conditions, principally climate, and population growth rates (Webb 1986; Woodward 1987; Gaston 2003). Similarly, evolutionary theory on species' ranges typically assumes that range margins are in equilibrium with current environments in order to examine the role of various evolutionary forces in limiting adaptation (e.g., Kirkpatrick and Barton 1997; Holt 2003; Case et al. 2005; Holt and Barfield 2011). Overall, these "equilibrial" range models would typically predict that species translocated beyond their range edges would likely fail to establish populations due to abiotic or biotic limits. Even with anthropogenic climate change, equilibrial range models would tend to suggest that shifts in the distribution of suitable habitat might occur only incrementally, limiting the potential for the types of large-scale translocations envisioned to ensure long-term species survival under new climatic regimes (Thomas 2011).

However, the applicability of equilibrial range models to small-ranged TDF plant species appears increasingly tenuous (e.g., Svenning and Skov 2004, 2007a,b; Schwartz et al. 2006; Van der Veken et al. 2007a). Specifically, for plant species with significant dispersal limitation, current range boundaries might not reflect fixed limits determined by environmental factors, but rather slow-moving colonization fronts influenced largely by species' dispersal rates, time since amelioration of past climatic stress, and the geographic locations of former refugia (Holt et al. 2005; Svenning and Skov 2007a,b; Bellemare 2010). Although the potential for long-term dispersal limitation of geographic ranges is not widely acknowledged by paleoecologists (e.g., Webb 1986; Prentice et al. 1991; Williams et al. 2001; but see Davis 1986), empirical evidence for this type of range "disequilibrium" (sensu Davis 1986) is increasing among TDF plant species (e.g., Holland 1980; Skov and Svenning 2004; Svenning and Skov 2004; Van der Veken et al. 2007b; Bellemare 2010). For example, Bellemare (2010) found that seeds of the ant-dispersed forest herb *Jeffersonia diphylla* (L.) Pers. germinated and successfully established over a five-year period in forest habitats 200 km beyond the species' natural range edge in the northeastern U.S. Similarly, Van der Veken et al. (2007b) presented data on an extra-range transplant experiment initiated almost 50 years earlier that showed long-term survival and expansion of *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. populations in areas up to ~ 100 km beyond its natural range edge in northwestern Europe. These empirical studies suggest that the extent of potentially suitable habitat for many dispersal-limited forest herbs may greatly exceed the area actually occupied (cf. Skov and Svenning 2004). Consequently, assisted colonization efforts for such species might be feasible over substantially greater spatial scales than would be predicted by standard equilibrial range models.

Other sources of information on plant species' climatic tolerances and the potential geographic scale of assisted colonization efforts are the many accidental or unplanned "experiments" evident in horticulture, where the climatic limits on numerous native plant species' distributions are routinely tested (Van der Veken et al. 2008; Sax et al. 2013). In particular, the horticultural trade includes numerous small-ranged forest species that are commonly grown many 100s to 1,000 km or more north of their natural ranges in eastern North America (Dirr 1998; Cullina 2000, 2002; Sax et al. 2013). Similarly, a review by Van der Veken et al. (2008) found that native plants were grown, on average, ~ 1,000 km north of their natural range edges in the horticultural trade in Europe. Although horticultural observations do not provide reliable information on the role that biotic factors (e.g., competitors, pollinators, pathogens, herbivores) might play in limiting the distributions of small-ranged plant species in the wild, they do demonstrate that climate per se is not limiting for many range-restricted species.

Even more strikingly, numerous incidences of small-ranged forest plant species escaping from horticulture and naturalizing in forest communities well beyond their range limits have been documented (Gleason and Cronquist 1991; Skov and Svenning 2004; Kartesz 2010). In Europe, a number of plant species endemic to areas around Pleistocene-era glacial refugia in southern and south-central Europe have been observed to readily naturalize in TDF forests of northwestern Europe (e.g., *Aesculus hippocastanum* L., *Aruncus dioicus* (Walter) Fernald,*Eranthis hyemalis* (L.) Salisb., *Lilium martagon* L., *Rhododendron ponticum* L.; Lid and Lid 1994; Stace 1997; Skov and Svenning 2004). Although such patterns have not been as extensively documented for forest plants in eastern North America, notable cases of small-ranged forest herbs and woody species naturalizing in areas far to the north of their natural ranges have been observed (e.g., *Aristolochia macrophylla* Lam., *Catalpa bignonioides* Walter, *Dicentra eximia* (Ker. Gawl.) Torr., *Leucothoe fontanesiana* (Steud.) Sleumer, *Torreya* *taxifolia*, *Trillium luteum* (Muhl.) Harbison; Gleason and Cronquist 1991; Case and Case 1997; Barlow and Martin 2004; Kartesz 2010). These various lines of evidence suggest that large-scale dispersal limitation may be a relatively common phenomenon among small-ranged TDF plants and, as a result, assisted colonization could be both a necessary and effective conservation strategy for some species.

OPEN QUESTIONS AND RESEARCH OPPORTUNITIES

It is evident that considerable research is still needed to better understand the magnitude of threat posed by modern climate change to forest herb biodiversity. Likewise, unconventional responses to these new conservation challenges, such as assisted colonization, will require substantial investigation before they should be considered for implementation (McLachlan et al. 2007; Minteer and Collins 2010; Sax et al. 2013). Here we outline what we see as some of the key open questions relating to small-ranged forest herbs, rapid climate change, and conservation.

First and foremost, a major research effort is needed to document and monitor existing populations of small-ranged TDF plant species in order to establish a baseline against which future population dynamics could be gauged. Because any attempts at intervention and translocation should be limited to species demonstrating clear evidence of climate-driven decline, basic descriptive research is needed on substantial numbers of plant species (e.g., species listed in appendix 21.1, as well as numerous woody TDF endemics). We are not aware of any demographic studies of forest herb populations, small-ranged species or otherwise, that have demonstrated declining population growth rates (i.e., $\lambda < 1$) at southern range margins in eastern North America, even though the biogeographic patterns detected in this and other studies suggest that such declines may be likely. Because these studies would be technically simple to conduct, albeit time-consuming, they could potentially be run simultaneously on multiple small-ranged TDF species to determine which, if any, should be considered as candidates for management, translocation, or other ex situ conservation options.

Second, in contrast to field-based demographic studies, molecular population genetic studies provide an opportunity to examine evidence of population dynamics across geographic ranges over substantially longer time scales (e.g., 100s–1,000s of years; reviewed in Moeller et al. 2011). If populations have expanded at northern range margins, but declined at southern range margins, these contrasting demographic histories should leave distinct signatures in samples of DNA sequences drawn from these populations. Although some forest plants have been the focus of phylogeographic studies using cpDNA haplotypes and population genetic studies focused on allozyme diversity (e.g., Griffin and Barrett 2004; MacLachlan et al. 2005; Gonzales et al. 2008), large datasets on nuclear DNA would be a substantially more powerful tool for uncovering demographic history. We are not aware of any studies that have yet used this approach to test hypotheses about demographic history in forest herbs.

Third, given that most analyses projecting plant species' responses to future climate change are based on models presuming distributional equilibrium with current climate (Huntley et al. 1995; Guisan and Thuiller 2005; Schwartz et al. 2006), there is a great need for more experimental research to directly test this assumption in forest herbs. Most notably, such efforts might include experimental seed-sowing within and beyond current range boundaries to assess plant performance and its relationship to environmental factors (e.g., Eckhart et al. 2004; Angert and Schemske 2005; Geber and Eckhart 2005; Griffith and Watson 2006; Van der Veken et al. 2007b; Bellemare 2010). Although northern range edges are a clear target for this type of investigation in light of the probable direction of future migration or assisted colonization efforts, there is also a significant need for further insight to the nature of species' southern, warm-margin distribution limits. If, as predicted by some ecological theory (MacArthur 1972), warm-margin range edges are determined primarily by biotic factors (e.g., competition, herbivory), rather than climate, there may actually be limited response to moderate levels of climate change, or species responses could be confounded or accelerated by complex biotic interactions (Van der Putten et al. 2010).

Fourth, whether forest herbs migrate naturally in response to climate change or threatened species are moved intentionally via assisted colonization, many forest plant communities will be colonized by new species in coming decades. Such intracontinental movements have received relatively little attention in the invasion biology literature, which has been focused primarily on invaders of intercontinental origin (e.g., Mack et al. 2000; chapter 12, this volume). It is not yet clear if intra- versus intercontinental invasions are directly comparable, but some evidence indicates that intracontinental movement of plants does not commonly lead to invasive behavior (Mueller and Hellman 2008; Simberloff et al. 2012). This difference might be due to a range of factors, for example, escape from natural enemies (e.g., pathogens, herbivores) is a key factor that has been linked to invasiveness among intercontinental exotics (Mitchell and Power 2003; Carpenter and Cappuccino 2005), but this ecological phenomenon may be less likely with intracontinental movements. An important focus for the types of forest herb seed-sowing experiments described above will be documentation of such biotic interactions within and beyond species' natural range limits. Insight into these biotic dynamics will be key to predicting species' migration potentials and evaluating risks associated with assisted colonization.

Finally, it has become clear that historical post-glacial range expansion has involved evolutionary change, not simply migration (Davis and Shaw 2001; Davis et al. 2005), and that populations migrating in response to modern climate change will likely experience natural selection on ecologically important traits (Geber and Dawson 1993; Etterson and Shaw 2001; Davis et al. 2005). For example, northward migration will involve substantial shifts in photoperiod (an important cue for development, dormancy, and flowering in many species), even if migrating populations were to perfectly track a particular set of climatic factors. It is important, then, to understand what genetic variation is currently harbored within and among populations in species' native ranges and how different genotypes may perform in novel northern environments. Identifying such genetic variation (e.g., through common garden experiments; cf. Fournier-Level et al. 2011) may be key to designing successful conservation efforts and preserving valuable intra-specific diversity in the future (Hampe and Petit 2005; McLachlan et al. 2007).

SUMMARY

Research increasingly indicates that dispersal limitation may be a major factor controlling the geographic distribution of numerous forest plant species and that the current distributions of many range-restricted species may still be strongly influenced by past episodes of climate change. The biogeographic patterns emerging from our survey of small-ranged forest herbs are highly consistent with this possibility, suggesting that many endemic species have exhibited relatively limited migration and range expansion during the Holocene. As many of these endemic species would be predicted a priori to be at increased risk from modern climate change due to small range size, the added challenge of long-term, large-scale dispersal limitation may significantly compound this risk (Thomas et al. 2004). Given these findings, modern climate change is likely to be a significant threat to forest herb biodiversity, and unconventional conservation options, like assisted colonization, may need to be considered for some particularly vulnerable forest herb species.

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APPENDIX 21.1

Range area, range centroid latitude and longitude, and habitat for 189 small-ranged forest herbs associated with Temperate Deciduous Forest in eastern North America. Nomenclature follows Kartesz (2010). Range statistics were derived from county-level distribution maps developed for each species by Kartesz (2010) and the Biota of North America Program (BONAP; see www.bonap.org). Habitat information was drawn from the *Flora of North America* for species covered by published volumes and from various regional sources (e.g., Radford et al. 1968; Gleason and Cronquist 1991; Case and Case 1997; Yatskievych 1999; Wunderlin and Hansen 2003; Weakley 2011).

Species	*Family*	*Range Area (km2)*	*Range Centroid Latitude (°)*	*Range Centroid Longitude (°)*	*Habitat Description*
Aconitum reclinatum A. Gray	Ranunculaceae	43681	37.736	80.554	Rich cove forests, seeps & shaded ravines, mtn woods
Aconitum uncinatum L.	Ranunculaceae	167349	37.011	81.422	Mesic woods, seeps & clearings
Actaea podocarpa DC	Ranunculaceae	107768	37.649	81.176	Moist, rich wooded slopes & coves
Actaea rubifolia (Kearney) Kartesz	Ranunculaceae	38063	36.564	85.945	Rich cove forests over calcareous bedrock
Ageratina luciae-brauniae (Fernald) King & H. Rob.	Asteraceae	11840	36.728	84.539	Shaded wet ledges, sandstone cliffs, “rockhouses”
Anemone lancifolia Pursh	Ranunculaceae	164761	36.171	80.675	Damp rich woods
Apios priceana B.L. Rob.	Fabaceae	48167	35.295	87.156	Rocky limestone woods
Astilbe biternata (Vent.) Britton	Saxifragaceae	90349	35.968	83.680	Rich woods, north-facing banks & seeps
Boechera perstellata (E.L. Braun) Al-Shehbaz	Brassicaceae	6767	36.855	85.985	Calcareous bluffs, wooded hillsides
Botrychium mormo W.H. Wagner	Ophioglossaceae	130069	46.635	91.286	Rich basswood & sugar maple forest
Boykinia aconitifolia Nuttall	Saxifragaceae	71430	36.256	83.296	Moist woodland, water edges
Cardamine flagellifera O.E. Schulz	Brassicaceae	29109	35.852	82.736	Moist wooded slopes, ravines, seeps
Cardamine micranthera Rollins	Brassicaceae	3770	36.412	80.239	Moist woods, along streams & seeps
Carex acidicola Naczi	Cyperaceae	11721	32.576	85.805	Dry to mesic deciduous forest
Carex austrocaroliniana L.H. Bailey	Cyperaceae	58524	35.339	84.677	Rich moist deciduous and mixed forest

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Species	*Family*	*Range Area (km2)*	*Range Centroid Latitude (°)*	*Range Centroid Longitude (°)*	*Habitat Description*
Carex basiantha Steudel	Cyperaceae	153979	31.691	89.115	Mesic to wet-mesic deciduous forests
Carex biltmoreana Mackenzie	Cyperaceae	20185	35.001	82.627	Rocky woods, moist ledges, granite balds
Carex brysonii Naczi	Cyperaceae	8677	33.541	87.709	Mesic deciduous forest, slopes above streams
Carex impressinervia Bryson Kral & Manhart	Cyperaceae	21699	32.604	86.166	Mesic deciduous forest, slopes above streams
Carex latebracteata Waterfall	Cyperaceae	22384	34.489	94.140	Steep shaded slopes, mesic to dry-mesic forest
Carex manhartii Bryson	Cyperaceae	26810	35.654	82.765	Moist deciduous and mixed forest
Carex ouachitana Kral Manhart & Bryson	Cyperaceae	19719	34.709	93.815	Mesic, dry-mesic rocky deciduous or mixed forest
Carex picta Steudel	Cyperaceae	106445	35.079	86.973	Forests & forest openings
Carex pigra Naczi	Cyperaceae	33105	34.541	85.530	Mesic to wet-mesic deciduous forests
Carex purpurifera Mack.	Cyperaceae	91720	36.981	84.201	Moist deciduous forests, often near limestone ledges
Carex radfordii Gaddy	Cyperaceae	6738	34.908	82.832	Moist deciduous forests on calcareous soil
Carex roanensis F.J. Herm.	Cyperaceae	25391	37.632	80.928	Rich moist soil under beech trees
Carex socialis Mohlenbr. & Schwegm.	Cyperaceae	138778	34.543	87.543	Lowland deciduous forests, clay soils
Carex superata Naczi, Reznicek & B.A. Ford	Cyperaceae	56149	33.926	84.342	Moist to dry-mesic open deciduous forests, ravines
Carex thornei Naczi	Cyperaceae	12881	31.586	84.898	Mesic deciduous forests, slopes & floodplains
Carex timida Naczi & B.A. Ford	Cyperaceae	30531	37.221	87.338	Mesic deciduous or mixed woods, calcareous soil
Chelone lyonii Pursh	Scrophulariaceae	48756	35.430	83.152	Rich coves, stream banks

Collinsonia tuberosa Michx.	Lamiaceae	156125	33.890	84.845	Moist woods, calcareous soils
Collinsonia verticillata Baldw.	Lamiaceae	104793	34.640	83.558	Wooded slopes, low woods
Corallorhiza bentleyi Freudenstein	Orchidaceae	4972	37.931	80.285	Deciduous forest & disturbed forest edges
Coreopsis delphiniifolia Lam.	Asteraceae	57448	33.195	81.577	Woodlands, thickets & swamps
Coreopsis latifolia Michx.	Asteraceae	37579	35.293	82.818	Shaded slopes in rich moist woods
Coreopsis pulchra Boynt.	Asteraceae	15001	33.938	86.160	Forest openings, outcrops
Croomia pauciflora (Nutt.) Torr.	Stemonaceae	118397	32.445	86.422	Mesic wooded slopes & bottoms, circumneutral soils
Cymophyllus fraserianus (Ker Gawl.) Kartesz & Gandhi	Cyperaceae	161869	37.209	81.412	Rich mesic shaded slopes in deciduous or mixed forest
Delphinium exaltatum Aiton	Ranunculaceae	150440	38.378	80.962	Rocky slopes in rich woods or barrens, calcareous soil
Delphinium newtonianum D.M. Moore	Ranunculaceae	15456	35.210	93.320	Slopes in deciduous forest
Desmodium humifusum (Muhl. Ex Bigelow) Beck	Fabaceae	60252	41.435	73.884	Dry woods, sandy soils
Desmodium ochroleucum M.A. Curtis ex Canby	Fabaceae	68327	36.163	82.393	Dry open woods, sandy or rocky soils
Dicentra eximia (Ker Gawl.) Torr.	Fumariaceae	113533	38.533	80.477	Dry to moist rocky mountain woods, cliffs & crevices
Diphylleia cymosa Michx.	Berberidaceae	30681	35.653	82.732	Moist slopes, seeps & stream banks in deciduous forest

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Species	*Family*	*Range Area (km2)*	*Range Centroid Latitude (°)*	*Range Centroid Longitude (°)*	*Habitat Description*
Dodecatheon amethystinum (Fassett) Fassett	Primulaceae	77954	41.491	88.342	Moist hillsides & limestone cliffs in deciduous forest
Dodecatheon frenchii (Vasey) Rydb.	Primulaceae	33569	36.935	88.144	Moist shaded flats in woods under cliffs, near streams
Draba ramosissima Desv.	Brassicaceae	189985	36.897	82.298	Rocky wooded areas, limestone cliffs, shale barrens
Elymus svensonii Church	Poaceae	15901	36.556	85.829	Woods on limestone bluffs, slopes & ledges
Erythronium propullans A. Gray	Liliaceae	8469	44.329	92.825	Mesic floodplain woods
Eupatorium godfreyanum Cronquist	Asteraceae	206635	37.821	80.203	Woods and disturbed open sites, forest edges
Euphorbia mercurialina Michx.	Euphorbiaceae	154614	34.917	84.759	Rich soil on wooded slopes, ravines
Euphorbia purpurea (Raf.) Fernald	Euphorbiaceae	65719	38.408	79.312	Dry or moist woods
Eurybia furcata (Burgess) G.L. Nesom	Asteraceae	144841	41.253	89.021	North-facing slopes, moist deciduous woods
Eurybia mirabilis (Torr. & A. Gray) G.L. Nesom	Asteraceae	36392	34.616	81.526	Deciduous & mixed woods, slopes or alluvial plains
Eutrochium steelei (E.E. Lamont) E.E. Lamont	Asteraceae	53807	36.108	82.830	Open woods, gravelly banks, thickets
Gentiana decora Pollard	Gentianaceae	147285	36.058	82.497	Wooded slopes, coves, streambanks
Geum geniculatum Michx.	Rosaceae	4251	36.105	81.832	Balds and wooded coves at high elevation
Gymnocarpium appalachianum Pryor & Haufler	Dryopteridaceae	63167	39.360	79.509	Maple-birch-hemlock woods, tallus w/ cold air seepage

Helianthus glaucophyllus D.M. Sm.	Asteraceae	31974	34.361	84.283	Moist forests, woodland edges
Heuchera longiflora Rydb.	Saxifragaceae	120569	36.636	83.826	Rich woods and roadcuts over limestone
Heuchera pubescens Pursh	Saxifragaceae	223208	37.923	81.327	Shaded circumneutral rock outcroppings in woods
Hexastylis contracta Blomquist	Aristolochiaceae	35994	36.444	83.544	Acid soils in deciduous woods
Hexastylis heterophylla (Ashe) Small	Aristolochiaceae	220495	35.921	82.539	Deciduous & mixed forests
Hexastylis lewisii (Fernald) Blomquist & Oosting	Aristolochiaceae	84708	36.178	78.893	Upland & lowland forests, floodplains
Hexastylis minor (Ashe) Blomquist	Aristolochiaceae	118466	36.385	79.880	Slopes & bluffs along streams in deciduous woods
Hexastylis naniflora Blomquist	Aristolochiaceae	13875	35.342	81.773	Acidic soils on bluffs & ravines in deciduous woods
Hexastylis rhombiformis Gaddy	Aristolochiaceae	5571	35.381	82.665	Deciduous woods on sandy river bluffs, ravines
Houstonia serpyllifolia Michx.	Rubiaceae	68074	35.968	82.651	Rich woods, stream margins, road cuts, pastures
Hydrophyllum brownei Kral & V.M. Bates	Hydrophyllaceae	14729	34.463	93.601	Rich deciduous forests
Liatris gholsonii L.C. Anderson	Asteraceae	3622	30.303	84.994	Slopes in deciduous woods, open xeric woods
Lilium grayi S. Watson	Liliaceae	27634	37.260	80.417	Moist forests, openings, bogs, seeps & wet meadows
Listera smallii Wiegand	Orchidaceae	137443	37.341	81.060	Damp humus in shady forests, under *Rhododendron*

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Species	*Family*	*Range Area (km2)*	*Range Centroid Latitude (°)*	*Range Centroid Longitude (°)*	*Habitat Description*
Lysimachia tonsa (Alph. Wood) Alph. Wood ex Pax & R. Knuth	Primulaceae	188779	35.454	83.082	Moist hardwood forests, pine-oak woods, bluffs
Matelea alabamensis (Vail) Woodson	Asclepiadaceae	12680	30.963	84.563	Slopes in deciduous forest
Matelea baldwyniana (Sweet) Woodson	Asclepiadaceae	91821	34.289	90.614	Open rocky woods, thickets
Matelea flavidula (Chapm.) Woodson	Asclepiadaceae	28298	32.215	83.229	Forested slopes & alluvial woods
Meehania cordata (Nutt.) Britton	Lamiaceae	280290	38.502	81.341	Rich mountain woods
Monotropsis odorata Schwein. Ex Elliott	Monotropaceae	117575	35.895	81.484	Mixed deciduous or coniferous forests
Napaea dioica L.	Malvaceae	144997	41.233	87.559	Moist alluvial woods
Onosmodium decipiens J. Allison	Boraginaceae	1595	32.997	87.124	Dolomite outcrops in rocky woods & glades
Orbexilum onobrychis (Nutt.) Rydb.	Fabaceae	211639	36.834	85.907	Open woods, prairies
Oxalis illinoiensis Schwegm.	Oxalidaceae	18788	37.076	86.559	Mesic to dry-mesic forests
Penstemon deamii Pennell	Scrophulariaceae	14461	38.374	87.972	Moist open woods, prairies
Penstemon smalli A. Heller	Scrophulariaceae	67622	35.223	84.115	Woodlands, cliffs, banks & forest edges
Penstemon tenuis Small	Scrophulariaceae	226272	32.491	92.333	Wet woodland soils, bottomlands
Phacelia covillei S. Watson	Hydrophyllaceae	18121	37.690	78.988	Rich soil of floodplains & alluvial woods
Phacelia fimbriata Michx.	Hydrophyllaceae	18475	35.225	84.269	Streambanks and alluvial woods
Phacelia gilioides Brand	Hydrophyllaceae	203809	36.851	93.099	Woodland openings, low rich woods, forest edges

Phacelia ranunculacea (Nutt.) Constance	Hydrophyllaceae	86316	36.495	89.531	Mesic alluvial forests
Platanthera integrilabia (Torr.)	Orchidaceae	71905	34.626	85.345	Wet wooded flats, seeps, wetlands
Polymnia cossatotensis Pittman & V.M. Bates	Asteraceae	4264	34.518	93.949	Upland rocky woods & tallus, chert outcrops
Polymnia laevigata Beadle	Asteraceae	32810	34.956	86.666	Damp shaded sites, calcareous soils
Prenanthes crepidinea Michx.	Asteraceae	214423	39.023	87.680	Moist rich deciduous woods, thickets, prairies
Prenanthes roanensis (Chickering) Chickering	Asteraceae	64373	36.042	82.453	Spruce-hardwood forests, wooded slopes & balds
Prosartes maculata (Buckley) A. Gray	Liliaceae	133520	36.723	83.839	Rich moist deciduous woods, slopes & ravines
Pycnanthemum beadlei (Small) Fernald	Lamiaceae	9218	36.036	82.318	Forests, woodland borders
Pycnanthemum curvipes (Greene) E. Grant & Epling	Lamiaceae	11002	35.505	83.566	Dry rocky woodlands, rock outcrops
Pycnanthemum loomisii Nutt.	Lamiaceae	167430	36.288	83.308	Forests, woodland borders
Pycnanthemum montanum Michx.	Lamiaceae	60612	36.036	82.721	Balds, woodlands, forests & forest edges
Pycnanthemum pycnanthemoides (Leavenworth) Fernald	Lamiaceae	224378	35.977	83.790	Forests, woodland borders
Pycnanthemum torrei Benth.	Lamiaceae	118144	38.117	80.876	Dry rocky woodlands
Ranunculus allegheniensis Britton	Ranunculaceae	228781	39.716	78.869	Moist or dry woods, pastures
Ranunculus harveyi (A. Gray) Britton	Ranunculaceae	181241	35.757	90.860	Acid soils on rocky wooded slopes, ridges, open areas

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Species	*Family*	*Range Area (km2)*	*Range Centroid Latitude (°)*	*Range Centroid Longitude (°)*	*Habitat Description*
Rudbeckia heliopsidis Torr. & A. Gray	Asteraceae	30072	34.134	82.963	Mesic to wet woodlands, meadows
Ruellia purshiana Fernald	Acanthaceae	96854	35.755	82.650	Dry woodlands over calcareous rock
Rugelia nudicaulis Shuttlw. ex Chapm.	Asteraceae	8435	35.416	83.423	High elevation spruce-fir & northern hardwood forest
Salvia urticifolia L.	Lamiaceae	222452	35.074	83.547	Rocky woodlands on circumneutral soils
Scirpus flaccidifolius (Fernald) Schuyler	Cyperaceae	5145	36.680	77.301	Wooded bottomlands
Scutellaria arguta Buckley	Lamiaceae	8601	37.422	82.573	Mesic woods and boulderfields at high elevation
Scutellaria montana Chapm.	Lamiaceae	11465	35.125	84.912	Open deciduous woods on mesic soil
Scutellaria pseudoserrata Epling	Lamiaceae	25289	34.273	85.258	Rich rocky forests
Scutellaria saxatilis Riddell	Lamiaceae	134303	37.039	82.940	Rocky forests, moist cliffs
Scutellaria serrata Andrews	Lamiaceae	160329	37.415	81.183	Rich deciduous forests
Sedum glaucophyllum R.T. Clausen	Crassulaceae	70801	36.266	80.519	Shaded cliffs, rocky slopes
Shortia galacifolia Torr. & A. Gray	Diapensiaceae	16960	35.255	82.715	Moist forest slopes & stream banks in deep shade
Silene catesbaei Walter	Caryophyllaceae	13101	32.253	84.080	Mesic deciduous forests along streams or slopes
Silene nivea (Nutt.) Muhl. Ex Otth	Caryophyllaceae	278558	40.581	86.336	Rocky or flood-scoured alluvial woodlands
Silene ovata Pursh	Caryophyllaceae	94821	33.975	86.367	Woodlands & forests on circumneutral soil
Silphium brachiatum Gattinger	Asteraceae	14651	35.098	86.501	Open forests on calcareous soil, roadcuts

Silphium wasiotense M. Medley	Asteraceae	7680	36.852	83.588	Dry open sites in mesic forests
Sisyrinchium dichotomum E.P. Bicknell	Iridaceae	6560	35.282	82.132	Dry to mesic oak-hickory forests
Solidago arenicola B,R, Keener & Kral	Asteraceae	4422	35.138	85.582	Mesic woods in deep sandy alluvium
Solidago auriculata Shuttlw. ex S.F. Blake	Asteraceae	132792	32.712	88.619	Rocky wooded slopes, alluvial soils
Solidago brachyphylla Chapman	Asteraceae	50576	32.068	84.767	Open woodlands, bluff forests
Solidago buckleyi Torrey & A. Gray	Asteraceae	46291	38.199	89.896	Open oak woods on ridges, slopes & bluffs
Solidago curtisii Torrey & A. Gray	Asteraceae	199625	36.086	83.685	Shaded mesic woods & thickets
Solidago drummondii Torrey & A. Gray	Asteraceae	5268	35.384	93.380	Limestone ledges & bluffs in rocky woods
Solidago faucibus Wieboldt	Asteraceae	27460	36.378	83.214	Mesic deciduous forests & hardwood-hemlock
Solidago flaccidifolia Small	Asteraceae	65118	34.581	85.173	Mesic woods & clearings
Solidago lancifolia (Torrey & A. Gray) Chapman	Asteraceae	4481	36.214	82.168	Rich woods, mountain slopes, road embankments
Solidago ouachitensis C.E.S. Taylor & R.J. Taylor	Asteraceae	12521	34.697	94.053	Woods on north-facing slopes
Solidago roanensis Porter	Asteraceae	166235	36.793	82.307	Forests, woodlands, roadbanks, edges of mtn balds
Solidago sphacelata Rafinesque	Asteraceae	210540	36.501	84.152	Open woods & rocky places, calcareous soils
Spigelia loganioides (Torr. & A. Gray ex Endl. & Fenzl) A. DC.	Loganiaceae	13586	29.101	82.055	Wet calcareous hammocks & woods

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Species	*Family*	*Range Area (km2)*	*Range Centroid Latitude (°)*	*Range Centroid Longitude (°)*	*Habitat Description*
Stachys clingmanii Small	Lamiaceae	22374	37.965	86.496	Cove forests & boulderfields at high elevation
Stachys cordata Riddell	Lamiaceae	205560	37.270	83.244	Moist forests, alluvial soils or over calcareous rock
Stachys eplingii J.B. Nelson	Lamiaceae	31266	36.409	82.080	Mtn woods, mesic forests, bogs & wet meadows
Stachys iltisii J.B. Nelson	Lamiaceae	29848	35.582	93.084	Rich soil in open upland woods
Stachys latidens Small ex Britton	Lamiaceae	55908	36.708	81.645	Mesic forests in coves, forest edges
Stellaria corei Shinners	Caryophyllaceae	127557	37.891	84.276	Mesic cove forests & seeps at mid- to high-elevation
Symphyotrichum anomalum (Engelm.) G.L. Neson	Asteraceae	245731	37.523	91.701	Rocky open deciduous woods, dry ridges, cliffs, bluffs
Symphyotrichum phlogifolium (Muhl. ex Willd.) G.L. Nesom	Asteraceae	229281	37.520	82.037	Rich mesic mixed hardwood forests, roadsides
Symphyotrichum retroflexum (Lindl. ex DC.) G.L. Nesom	Asteraceae	64470	34.405	83.084	Moist woodlands, meadows, open pine or oak woods
Synandra hispidula (Michx.) Britton	Lamiaceae	121940	38.105	84.694	Rich mesic woods
Thalictrum clavatum DC.	Ranunculaceae	105376	36.293	83.545	Rich moist woods, cliffs, seeps, stream banks
Thalictrum coriaceum (Britton) Small	Ranunculaceae	92381	37.382	81.760	Rocky or mesic open deciduous woods, thickets
Thalictrum debile Buckley	Ranunculaceae	28466	33.444	87.312	Rich, rocky woods on limestone, wet alluvial soil
Thalictrum macrostylum Small & A. Heller	Ranunculaceae	81502	34.951	80.734	Rich wooded slopes, cliffs, swamp forests, meadows
Thalictrum mirabile Small	Ranunculaceae	15112	35.523	86.089	Moist bluffs, wet sandstone cliffs, sinks

Thaspium pinnatifidum (Buckley) A. Gray	Apiaceae	15560	36.586	84.752	Forests & woodlands over calcareous rock
Thermopsis fraxinifolia Nutt. ex M.A. Curtis	Fabaceae	42342	34.942	83.022	Dry slopes, ridges & clearings
Thermopsis mollis (Michx.) M.A. Curtis ex A. Gray	Fabaceae	80831	35.746	82.320	Dry slopes, open woods & clearings
Thermopsis villosa (Walter) Fernald & B.G. Schub.	Fabaceae	37056	35.877	82.885	Mesic forest openings, floodplains & roadbanks
Tragia cordata Michx.	Euphorbiaceae	172584	33.632	89.576	Rich woods over limestone, rocky hillsides
Trifolium stoloniferum Muhl. ex Eaton	Fabaceae	102702	38.140	87.699	Moist disturbed forests, streams, open woods, lawns
Trillium decipiens J.D. Freeman	Melanthiaceae	41712	31.828	84.671	Rich woods & river bluffs in mixed deciduous forests
Trillium decumbens Harbison	Melanthiaceae	38956	33.870	85.463	Rocky slopes in open deciduous woodlands
Trillium discolor Wray ex Hook.	Melanthiaceae	15733	34.339	82.551	Forested slopes & stream banks
Trillium foetidissimum J.D. Freeman	Melanthiaceae	71867	31.105	92.228	Rich woods on river bluffs, floodplains, roadsides
Trillium gracile J.D. Freeman	Melanthiaceae	47927	31.009	94.179	Mature pine & hardwood forests, slopes near streams
Trillium lancifolium Raf.	Melanthiaceae	68672	33.317	85.249	Floodplain forests, rocky upland woods & thickets
Trillium ludovicianum Harbison	Melanthiaceae	61448	31.552	92.487	Mixed deciduous floodplain woods & adj. slopes
Trillium luteum (Muhl.) Harbison	Melanthiaceae	71780	34.354	83.826	Rich deciduous forest & open woods, calcareous soils

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Species	*Family*	*Range Area (km2)*	*Range Centroid Latitude (°)*	*Range Centroid Longitude (°)*	*Habitat Description*
Trillium maculatum Raf.	Melanthiaceae	92959	31.660	83.938	Rich mesic forests, river banks & bluffs, floodplains
Trillium oostingii Gaddy	Melanthiaceae	1742	34.352	80.583	Rich bottomland forests
Trillium persistens Duncan	Melanthiaceae	2970	34.755	83.198	Mixed deciduous & pine woodlands, stream flats
Trillium pusillum Michx.	Melanthiaceae	92822	36.115	85.434	Dry to mesic forests, along streams, swampy woods
Trillium reliquum J.D. Freeman	Melanthiaceae	26511	32.315	84.163	Rich mixed forest, slopes, bluffs & stream flats
Trillium rugelii Rendle	Melanthiaceae	91092	35.133	83.850	Rich deciduous forests, calcareous or mafic bedrock
Trillium simile Gleanon	Melanthiaceae	26375	35.307	83.421	Forested coves, slopes & seeps with rich soil
Trillium stamineum Harbison	Melanthiaceae	97060	33.645	87.520	Upland deciduous forest over limestone, floodplains
Trillium sulcatum Patrick	Melanthiaceae	99413	38.779	80.968	Coves & moist slopes, rich mesic woodlands
Trillium underwoodii Small	Melanthiaceae	75918	31.587	85.220	Dry to mesic rich deciduous forests, stream edges
Trillium vaseyi Harbison	Melanthiaceae	36463	33.210	84.492	Steep wooded slopes, rich coves & ravines
Trillium viride Beck	Melanthiaceae	41016	38.471	90.572	Rich woods, bluffs & rocky hillsides
Trillium viridescens Nutt.	Melanthiaceae	120456	34.685	93.618	Rich deciduous forests, bluffs & floodplains
Uvularia floridana Chapm.	Liliaceae	48386	32.203	84.840	Rich hardwood forests, floodplains & moist ravines
Valeriana pauciflora Michx.	Valerianaceae	213927	38.998	84.412	Rich mesic woods

Veratrum latifolium (Desr.) Zomlefer	Liliaceae	164689	36.651	81.255	Moist to dry forests
Veratrum parviflorum Michx.	Liliaceae	110403	35.900	83.904	Moist wooded slopes, dry forests
Veratrum woodii J.W. Robbins ex Alph. Wood	Liliaceae	183745	37.339	87.774	Rich woods on circumneutral soil
Vernonia arkansana DC.	Asteraceae	188301	39.133	93.390	Low woods, streambanks, roadsides
Viola tripartita Elliott	Violaceae	214221	35.650	83.407	Rich woods, moist slopes, bottomlands
Viola villosa Walter	Violaceae	251059	33.182	88.085	Moist sandy or rocky soil, hardwood hammocks
Waldsteinia lobata (Baldw.) Torr. & A. Gray	Rosaceae	16248	33.792	83.900	Forests, streambanks
Xerophyllum asphodeloides (L.) Nutt.	Liliaceae	86181	36.641	81.026	Forests on dry ridges & slopes, pine barrens
Zizia trifoliata (Michx.) Fernald	Apiaceae	228512	34.441	83.091	Mesic forest, woodlands, forest edges

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