

# Fine-scale environmental heterogeneity and spatial niche partitioning among spring-flowering forest herbs

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Manuscript received 20 June 2020; revision accepted 14 September 2020.

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**Citation:** Beck, J. J. and T. J. Givnish. 2021. Fine-scale environmental heterogeneity and spatial niche partitioning among spring-flowering forest herbs. *American Journal of Botany* 108(1): 63–73.

doi:10.1002/ajb2.1593

**PREMISE:** Environmental heterogeneity influences plant distributions and diversity at several spatial scales. In temperate forests, fine-scale environmental variation may promote local coexistence among herbaceous species by allowing plants to spatially partition microsites within forest stands. Here we argue that shallow soils, low soil water-holding capacity and fertility, and reduced light near tree boles should favor short, shallow-rooted, evergreen species like *Anemone acutiloba* with low moisture, nutrient, and light requirements. Farther from trees, richer, deeper soils should favor taller, deeper-rooted herbs with greater moisture and nutrient demands, such as *Sanguinaria canadensis* and *Trillium flexipes*.

**METHODS:** We tested these hypotheses by mapping the fine-scale distributions of *Anemone*, *Sanguinaria*, and *Trillium* individuals within a 50 × 50 m plot, comparing local species' distributions with respect to soil depth and proximity to neighboring trees, and characterizing intraspecific and interspecific spatial associations.

**RESULTS:** Local plant distributions were consistent with our predictions based on leaf height, physiology, and phenology. *Anemone* was found in microsites on shallower soils and closer to trees than either *Sanguinaria* or *Trillium*. In all three species, individual plants were spatially aggregated within 2 m, but spatially segregated from individuals of the other species beyond 2 m.

**CONCLUSIONS:** Differential plant responses to fine-scale environmental heterogeneity and observed spatial associations suggest that local species-environment associations could facilitate coexistence. These findings illustrate how fine-scale environmental heterogeneity coupled with phenological and physiological differences likely contribute to spatial niche partitioning among spring-flowering forest herbs and maintain high local plant diversity within temperate forests.

**KEY WORDS** environmental heterogeneity; coexistence; temperate forest; soil depth; understory; *Anemone acutiloba*; *Sanguinaria canadensis*; *Trillium flexipes*.

Environmental heterogeneity plays an important role in determining plant distributions and maintaining species diversity across a range of spatial scales (Ricklefs, 1977; Amarasekare, 2003; Krefth and Jetz, 2007; Bartels and Chen, 2010; Costanza et al., 2011; Stein et al., 2014). At broad spatial scales, plant distributions vary with climate, edaphic conditions, and other abiotic factors (Krefth and Jetz, 2007). This environmental variation is positively associated with species richness and has been implicated as an important factor maintaining regional diversity (Ricklefs, 1977; Krefth and Jetz, 2007; Stein et al., 2014). Environmental heterogeneity can also influence plant distributions at finer scales (Lundholm, 2009; Bartels and Chen, 2010; Costanza et al., 2011; Catella et al., 2019). Yet, few empirical

studies carefully consider the physiological differences and competitive interactions underlying differential species responses to local environmental heterogeneity (Silvertown, 2004) or the spatial scales at which this local heterogeneity could facilitate coexistence (Amarasekare, 2003; Kneitel and Chase, 2004; Lundholm, 2009; Tamme et al., 2010; Hart et al., 2017).

Terrestrial plant species compete for a limited set of finite resources including water, light, and a suite of macronutrients (Silvertown, 2004). Interspecific tradeoffs in resource acquisition and use are expected to stabilize coexistence when differential resource limitation increases intraspecific competition relative to interspecific competition (Tilman, 1982; Chesson, 2000b).

However, it remains unclear whether there are enough limiting resources or sufficiently strong tradeoffs for such complementary resource use alone to maintain high local plant diversity in an otherwise homogeneous environment (Goldberg and Barton, 1992; Silvertown, 2004; Adler et al., 2010; Kraft et al., 2015). In contrast, there is ample evidence that coexistence is facilitated by differential plant responses to environmental variation in space (Amarasekare, 2003; Silvertown, 2004; Bartels and Chen, 2010; Stein et al., 2014) and time (Chesson and Warner, 1981; Levine and Rees, 2004; Adler et al., 2006; Angert et al., 2009). The potential for spatial heterogeneity to promote coexistence, however, depends critically on the scale of heterogeneity relative to the dispersal capacity of competing plants and how strongly plant performance varies with the environment (Chesson, 2000a; Snyder and Chesson, 2004). An improved understanding of the physiological characteristics underlying differential plant responses to environmental variation and careful examination of local plant distributions are important for assessing potential for fine-scale environmental heterogeneity to maintain local plant diversity in natural communities (Kneitel and Chase, 2004; Silvertown, 2004; Lundholm, 2009; HilleRisLambers et al., 2012; Hart et al., 2017). Specifically, examining whether fine-scale species–environment associations are predictable and conform to theoretical expectation based on physiological differences, can provide insights into the processes shaping local plant distributions. Likewise, evaluating intraspecific and interspecific spatial associations in natural plant communities can elucidate whether the net effect of competitive interactions, environmental sorting, and dispersal reinforces interspecific spatial segregation (an important prerequisite for spatial variation to facilitate coexistence) or if instead, it tends to scramble species–environment relationships.

Characterizing the potential for fine-scale environmental heterogeneity to structure local plant distributions and promote coexistence is especially important in plant communities with high local plant diversity. One intriguing case involves the coexistence of large numbers of herbaceous plants in temperate deciduous forests. Herbaceous taxa comprise approximately 80% of plant species in such forests (Gilliam, 2007). Between 50 and 100 understory species regularly coexist within a single hectare, and 10–15 such species may co-occur within 1 m<sup>2</sup> (Gilliam, 2007; Rogers et al., 2008; Peet et al., 2014). Environmental variation shapes the distribution of herbaceous species in temperate deciduous forests at multiple spatial scales (Gilbert and Lechowicz, 2004; Bartels and Chen, 2010; Costanza et al., 2011; Beatty, 2014; Peet et al., 2014). At broad spatial scales along environmental gradients, the distribution and abundance of understory herbaceous species vary in response to covarying biotic and abiotic factors (Whittaker, 1956; Curtis, 1959; Leach and Givnish, 1999; Gilbert and Lechowicz, 2004; Amatangelo et al., 2014; Beatty, 2014; Burton et al., 2014; Peet et al., 2014; Gilliam et al., 2016). Differential plant responses to these broad environmental gradients reflect physiological tradeoffs and strategies adapted for different environmental conditions (Givnish, 1982, 1987, 1995; Amatangelo et al., 2014; Neufeld and Young, 2014).

Understory plant species also respond sensitively to environmental variation at finer spatial scales. Within forest stands, herbaceous plant species often exhibit highly heterogeneous spatial distributions and these local distributions reflect, in part, fine-scale variation in the environment (Struik and Curtis, 1962; Anderson et al., 1969; Burton et al., 2011; Sabatini et al., 2014; Chudomelová et al., 2017; Catella et al., 2019). For example, fallen trees create light

gaps in otherwise closed canopy forests, which favor the growth of certain herbaceous species (Thompson, 1980). Treefalls can also create microtopographic heterogeneity, which influences the distribution of distribution of herbaceous species independent of light availability (Beatty, 1984; Beatty and Stone, 1986; Moore and Vankat, 1986; Peterson et al., 1990; Scheller and Mladenoff, 2002; Graves et al., 2006). Trees overhead can influence the distribution of understory plant species by modifying the physical environment and modulating the flow of resources through forest ecosystems (Augusto et al., 2003; Barbier et al., 2008). Variation in how readily trees transmit light to the forest floor (Canham and Burbank, 1994), the seasonal timing of light availability (Lopez et al., 2008), rates and nutrient concentrations of stem-flow (Crozier and Boerner, 1984), and differences in resource uptake (e.g., because of shallower roots) and litter characteristics among tree species (Finzi et al., 1998) can all affect the distribution and growth of understory plants.

Linking local plant distributions to niche differences requires considering plant distributions relative to underlying environmental variation as well as differences in plant morphology and physiology. In a classic study of within-stand distributions of forest herbs, Bratton (1976) found that herb species composition varied with proximity to canopy trees as well as exposed bedrock and boulders. Bratton (1976) argued that soil depth and plant rooting depth helped determine species distributions. Herbs with shallow, fibrous root systems were more abundant on or near boulders and the bases of trees, whereas plants with more substantial bulbs and rhizomes and deeper roots were physically unable to establish themselves in such microsites with shallow soil. Yet soil depth is not the only factor that varies near tree trunks. Light levels near tree boles should be greatly reduced, especially in midsummer, because of the boles blocking all light from nearly half the sky, and with little reflected light when tree canopies have flushed. Low light levels should reduce total herb cover (Givnish, 1982) and on mesic sites favor evergreens with longer periods to amortize leaf construction costs (Givnish, 2002). Increased stemflow can wash away soil from around the trunk, especially fine particles that contribute to moisture and nutrient supply, and leach soils (Levia and Frost, 2003; Barbier et al., 2008). However, the effects of nutrient leaching might be nullified or even reversed in some cases because of greater nutrient concentrations in stemflow vs. throughflow (Crozier and Boerner, 1984; Andersson, 1991) or greater N mineralization rates near bole (Boerner and Koslowsky, 1989). More predictably, decreased soil depth due to large shallow tree roots should restrict soil moisture and nutrient supplies near tree boles; this—combined with the lower light levels near the trunk (see above)—should also result in sparser herb cover. Finally, in cool or cold temperate forests, snow melts earlier from areas immediately adjacent to tree boles, extending the potential growing season for understory herbs there (Vellend et al., 2017). Consequently, in sparsely covered sites on thin soils near tree boles, we would expect herbs with shallower roots, leaves held closer to the ground (Givnish, 1982, 1987, 1995), and a greater tendency toward the evergreen habit—here associated with poor soils and a longer growing season (Givnish, 2002)—compared with taller, more deeply rooted species growing in more densely covered microsites on deeper soils farther away. These considerations provide testable insights into the fine-scale distribution of forest herbs and some ecological processes responsible for maintaining understory plant diversity (Collins et al., 1984).

Here we describe the local distribution of three common, spring-flowering forest herbs: *Anemone acutiloba*, *Sanguinaria*

*canadensis*, and *Trillium flexipes*. Although these species commonly co-occur in North American forests and share ecological characteristics typical of temperate forest herbs, the three focal species differ with respect to several key physiological characteristics, especially leaf height, leaf nutrient demands, rooting depth, and leaf phenology (Table 1). We address three primary questions: (1) Does fine-scale environmental heterogeneity influence the local distributions of these three species? (2) Are differences in their responses to local environmental variation linked to interspecific phenotypic differences in accord with theory? (3) Do these forest herbs exhibit interspecific spatial segregation within forest stands? Differences in rooting depth, photosynthetic phenology, leaf height, and resource requirements should influence the local distribution of plants and cause fine-scale spatial segregation. We hypothesized that *Anemone* (with evergreen leaves, short stature, shallow fibrous roots, and low nutrient requirements) should occur on shallower soils and/or closer to trees than the taller, more deeply rooted, more nutrient-demanding spring- and summer-active *Sanguinaria* and *Trillium*, which should competitively exclude *Anemone* from microsites with deeper soils farther from trees.

## MATERIALS AND METHODS

### Study site

We conducted studies at McGilvra Woods State Natural Area (Sauk County, Wisconsin, USA), a 26-ha forest stand managed by the Wisconsin Department of Natural Resources (Appendix S1). The stand is located within the Baraboo Hills, a 216 km<sup>2</sup> region marked by remnants of an ancient mountain range composed of uplifted Precambrian quartzite, which rises roughly 200 m above the surrounding area in south-central Wisconsin. This area is considered a regional conservation priority that encompasses the largest tract of contiguous forest in southern Wisconsin and supports more than 1300 plant species (Lange, 1998). McGilvra Woods lies near the center of the Baraboo Range. Our 50 × 50 m forested study plot slopes gently (2–6%) to the northwest. Soils consist of Fayette and La Farge silt loams derived from loess deposits. Our study plot is dominated by *Acer saccharum* (40% of tree basal area; Appendix S2) with *Quercus rubra* (22%), *Tilia americana* (17%), *Fraxinus americana* (10%), *Carya cordiformis* (5%), *Quercus alba* (4%), *Prunus serotina* (1%), and *Ulmus americana* (<1%) as subdominant canopy trees. The understory includes a rich diversity of herbaceous plant species

including several spring ephemerals (*Cardamine concatenata*, *C. douglasii*, *Claytonia virginica*, *Erythronium albidum*, *E. americanum*) and early-summer species (sensu Givnish 1987—*Actaea rubra*, *Enemion biternatum*, *Hydrophyllum virginianum*, *Mitella diphylla*, *Phlox divaricata*, *Thalictrum dioicum*, and *Uvularia grandiflora*).

We focused on three species common to forests throughout eastern North America: *Anemone acutiloba* DC., *Sanguinaria canadensis* L., and *Trillium flexipes* Raf—hereafter referred to as *Anemone*, *Sanguinaria*, and *Trillium*. All three focal species flower in spring and have elaiosomes that are primarily dispersed by ants (Pudlo et al., 1980; Handel et al., 1981; Smith et al., 1989). However, these species differ in leaf phenology, stature, nutrient requirements, and other relevant physiological characteristics (Table 1; Appendix S3). *Anemone* is relatively short-statured (leaves held <15 cm above ground) and has evergreen leaves that senesce after one year. This species has relatively low nutrient demands (2.1% leaf N content, Table 1) and possesses a shallow, fibrous root system. *Sanguinaria* leafs out early for an early-summer species, with leaves unfolding into a fully umbrella-like form 15–35 cm tall around the time of canopy closure in mid-May and persisting through midsummer. Compared with *Anemone*, *Sanguinaria* has extensive fibrous roots that extend from a thickened belowground rhizome, taller leaf height (typically 15–35 cm), and—based on larger leaves with higher nutrient concentrations—higher nutrient demands (2.9% leaf N content). *Trillium* is also an early-summer species, but its leaves emerge a bit later than *Sanguinaria* and are taller (25–50 cm). *Trillium* also has greater nutrient demands (3.9% leaf N content) and possesses a thickened rhizome with a more extensive system of fibrous roots growing from the rhizome.

### Field methods

In May 2019, we mapped the distribution of all *Anemone*, *Sanguinaria*, and *Trillium* within a 50 × 50 m plot. This focal plot was embedded within a larger 1-ha forest monitoring plot in which all trees greater than 1 cm diameter at breast height (DBH) are permanently marked, mapped, and identified to species (Appendix S4). The 50 × 50 m focal plot included 110 trees of eight species (Appendix S2). After delineating plot boundaries, we systematically searched the plot for the focal herb species and temporarily marked the location of each plant (Fig. 1). For the purposes of this study, we considered as separate individuals for mapping all stems greater than 10 cm apart and not obviously connected to nearby stems by

**TABLE 1.** Comparison of relevant ecological and physiological characteristics among focal forest plant species. Mean leaf height (cm) and leaf N content (percentage by mass) derived from the UW-Madison Plant Ecology Laboratory trait database (Amatangelo et al., 2014; Sonnier et al., 2014).

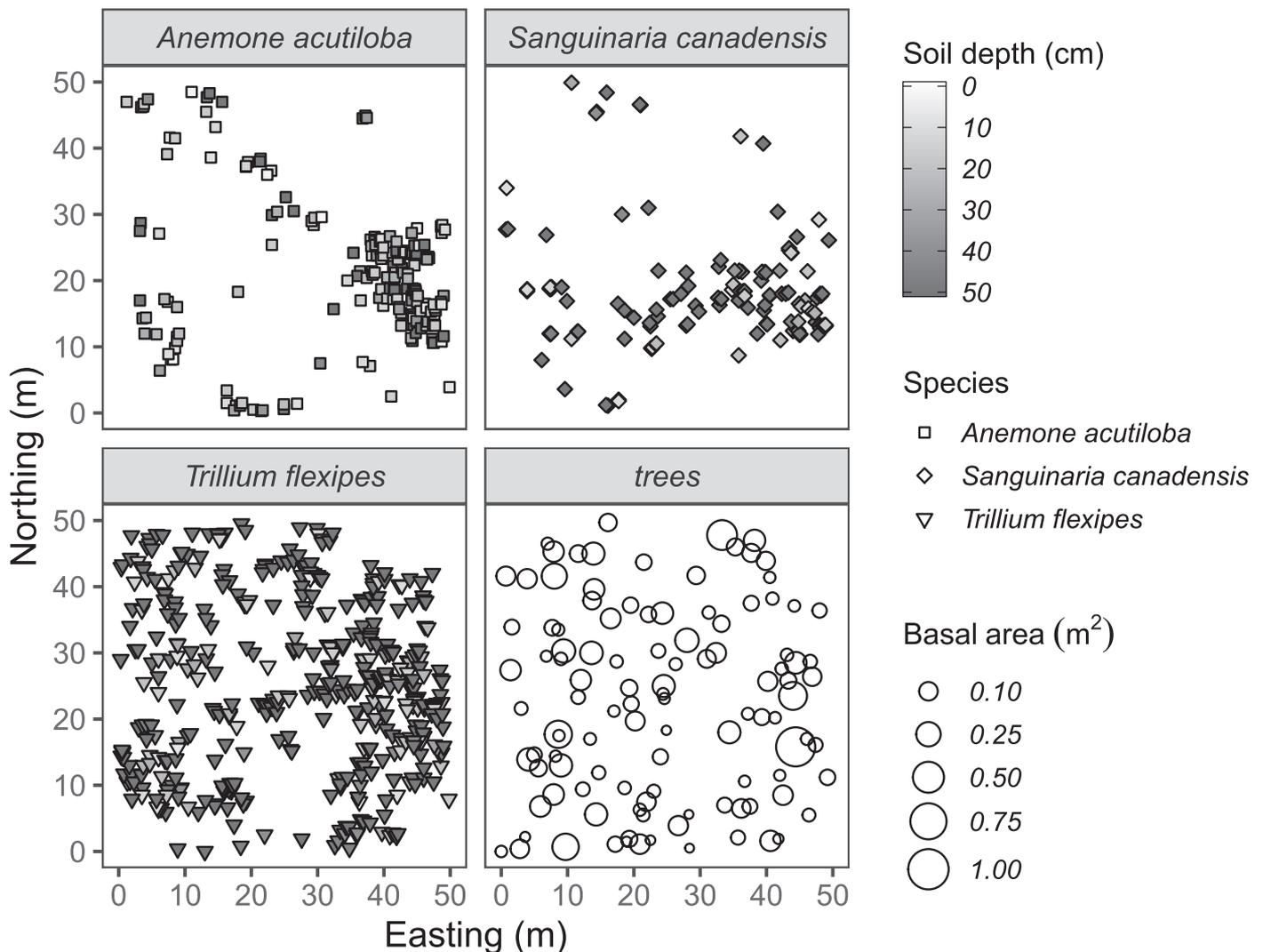
	Focal species		
	<i>Anemone acutiloba</i>	<i>Sanguinaria canadensis</i>	<i>Trillium flexipes</i>
Family	Ranunculaceae	Papaveraceae	Melanthiaceae
Flowering phenology	Early spring (March–May)	Early spring (March–May)	Early summer (May–June)
Leaf (photosynthetic) phenology	One-year evergreen (retains leaves for one full year)	Early Summer (leaves emerge during flowering period but open in May and persist through midsummer)	Early summer (leaves emerge in May and persist through midsummer)
Rooting physiology	Shallow, fibrous root system	Deeper fibrous roots extending from thickened rhizome	Deeper fibrous roots extending from thickened rhizome
Leaf height (mean)	<15 cm (11.9)	15–35 cm (25.3)	25–50 cm (32.1)
Nutrient demands (leaf N percent by mass)	Low (2.1%)	Intermediate (2.9%)	High (3.9%)
Seed dispersal mode	Ant (elaiosomes)	Ant (elaiosomes)	Ant (elaiosomes)

rhizomes. We then split the plot into 5-m wide strips, re-searched each segment to ensure no plants were missed, and mapped the location of each individual plant within the plot with ~10 cm precision. In addition to mapping focal plants, we used a 2.6 mm diameter metal wire to probe the soil at the base of each stem and estimated soil depth (to the nearest centimeter, maximum of 50 cm). We also measured the distance from each focal individual to the nearest live or dead tree stem (0.1 m precision). Finally, we measured soil depth every 2.5 m along 11 50-m east-west transects spaced 5 m apart to obtain a reference distribution of background soil depths within the plot.

### Data analysis

To test whether the focal species tended to segregate into different environmental microsites, we analyzed differences in their distributions with respect to soil depth and proximity to neighboring trees. We used a spatial analysis of variance (ANOVA) to test for

differences in mean soil depth among focal species while accounting for nonindependence of residuals caused by spatial autocorrelation (Zuur et al., 2009). This model included observed soil depths for all focal species and the reference sample of background soil depths, which allowed us to test for differences among species as well as differences between focal species and the soil depth expected if plant species occur at random with respect to the background environmental conditions. We examined spatial dependence in soil depth using semivariogram analysis (Bivand et al., 2013). Exponential-, Gaussian-, and spherical correlation structures provided similar fits for the spatial dependence among residuals, so we used an exponential correlation structure in our spatial ANOVA to account for spatial dependencies in soil depth within the plot (Zuur et al., 2009). To examine whether species were distributed differently with respect to trees, we used an ANOVA to test for variation among focal species in their proximity to the nearest tree. In this model, we did not include a term for residual spatial covariance because the dependent variable—distance to nearest tree—is itself a spatial measurement.



**FIGURE 1.** Map illustrating the spatial distribution of *Anemone acutiloba*, *Sanguinaria canadensis*, *Trillium flexipes*, and trees greater than 1 cm DBH within a 50 × 50 m plot at McGillvra Woods State Natural Area (Sauk County, Wisconsin, USA). Each point represents the location of a focal herb or tree. The Easting and Northing coordinates measure the distance in meters from the origin (southwest corner) of the plot. Herb points are shaded according to the measured soil depth and the size of tree circles is proportional to its basal area.

We also examined how proximity to neighboring trees varied with tree size. After grouping trees into large (>25 cm DBH) and small (<25 cm DBH) size classes, we used a linear model that included a random effect for herb individuals to test for differences among herb species, between tree size classes, and the interaction between herb focal species and tree size class.

We next explored spatial associations among conspecific individuals, between pairs of focal species, and between each focal species and neighboring trees using pair correlation functions (PCFs). PCFs describe the probability of observing a pair of points at a particular distance divided by the expected probability under complete spatial randomness,  $g(r)$  (Wiegand and Moloney, 2014). Whereas related metrics rely on cumulative point densities at successively larger radii to infer spatial patterns (thus patterns at a given radius depend on point densities at smaller radii), spatial patterns inferred from PCFs do not necessarily exhibit spatial dependence across scales and thus lend themselves to more straightforward interpretation (Wiegand and Moloney, 2004).

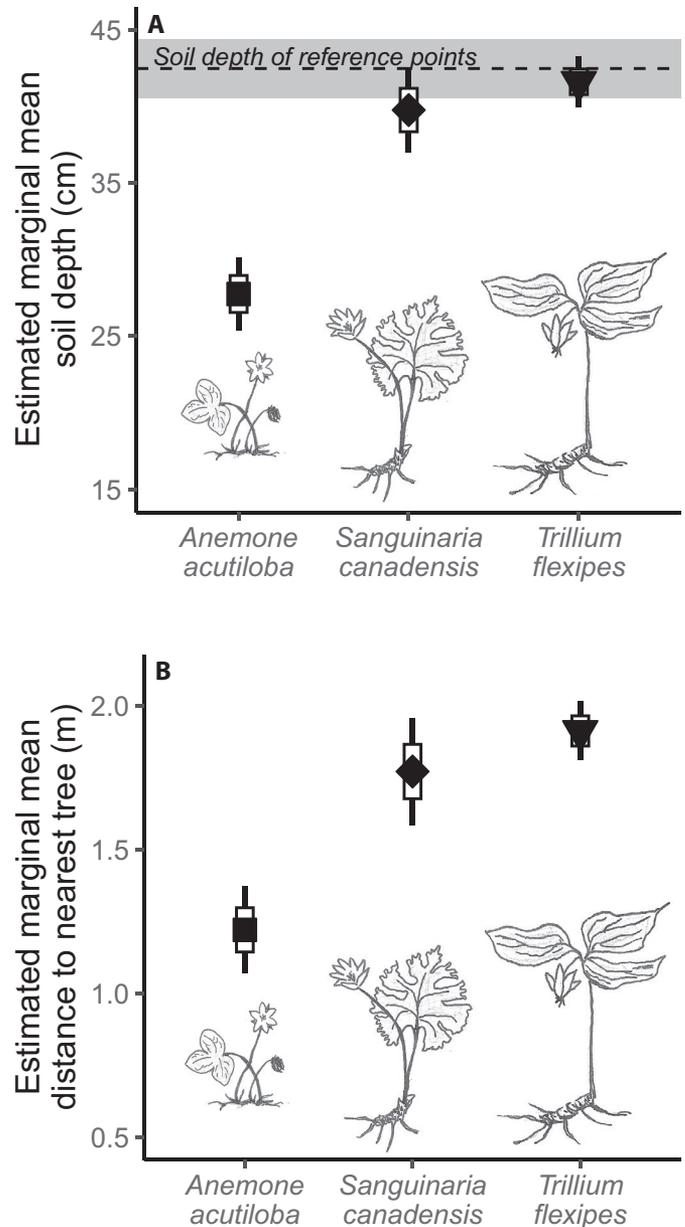
For all analyses, we used inhomogeneous pair correlation functions,  $g_{\text{inhom}}(r)$ , which allow the density of individuals to vary in space independent of proximity to events via a nonstationary Poisson process (Wiegand and Moloney, 2014). We applied Ripley's isotropic edge correction to reduce estimation bias caused by edge effects. This method weights the influence of spatial events on estimated PCFs according to their proximity to the plot boundary (Wiegand and Moloney, 2004, 2014; Baddeley, 2005). In the first set of point pattern analyses, we explored how the observed density of individuals belonging to a given focal species varied with proximity to conspecific individuals. In the second set of spatial analyses, we investigated how the probability of encountering individuals of a given focal species varied with proximity to heterospecific individuals for each pair of species. Finally, we characterized how the probability of encountering individuals belonging to a given focal species varied with proximity to neighboring trees. For each PCF, we calculated a simulation envelope (499 iterations) for expected  $g_{\text{inhom}}(r)$  values under complete spatial randomness. Observed  $g_{\text{inhom}}(r)$  values that fall outside the simulation envelope can be interpreted as statistically significant deviations from spatial randomness (Wiegand and Moloney, 2014).

All analyses were performed using R 3.5.1 (R Core Team, 2016). Spatial linear models were performed using the  $gls$  function in the 'nlme' package (Pinheiro et al., 2020) and semivariograms were fit using the 'gstat' package (Pebesma, 2004). PCFs describing conspecific spatial associations were performed using the  $pcf_{\text{inhom}}$  function and PCFs describing heterospecific spatial associations were performed using the  $pcf_{\text{cross.inhom}}$  function within the 'spatstat' package (Baddeley, 2005). The package 'ggplot2' was used for generating figures (Wickham, 2016).

## RESULTS

Our 50 m × 50 m study plot contained 201 individuals of *Anemone*, 133 of *Sanguinaria*, and 433 of *Trillium*. While the density of *Trillium* was fairly consistent across the plot, *Sanguinaria* and *Anemone* were more patchily distributed (Fig. 1). These distributional differences among focal species reflected variation in soil depth and proximity to neighboring trees (Fig. 2). *Anemone* occurred more frequently at shallow soil depths compared to *Sanguinaria*, *Trillium*, and the background distribution of soil

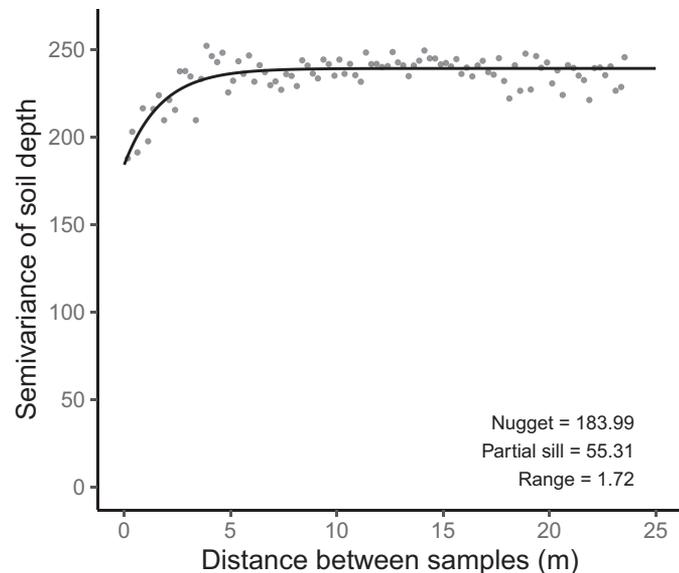
depth within the plot (Fig. 2A; Spatial ANOVA:  $F_{3, 993} = 45.799$ ,  $P < 0.001$ ). Only 21% of *Anemone* individuals occurred at soil depths greater than 50 cm while 56% of *Sanguinaria* and 66% of *Trillium* were located in microsites with soil depths greater than 50 cm. *Anemone* was restricted to shallower soils than the reference distribution of soil depths within the plot:  $27.8 \pm 1.2$  (SE) cm for *Anemone* vs.  $42.5 \pm 1.0$  cm for the background. We found no evidence that the soil depth distributions of *Trillium* ( $41.6 \pm 0.8$  cm)



**FIGURE 2.** Estimated marginal means for (A) soil depth and (B) proximity to nearest tree for each focal species. The statistical model examining comparative soil depth accounted for spatial covariance. Black bars represent 95% confidence intervals and white bars represent one standard error of the estimated marginal mean. The dashed line represents the estimated marginal mean of soil depth for reference points within the focal plot and the gray shaded area illustrates a 95% confidence interval for the reference points. Illustrations courtesy of M. Persche.

and *Sanguinaria* ( $39.8 \pm 1.4$  cm) differed from one another. These results suggest that on average, *Sanguinaria* was found in slightly shallower soil than expected from the reference distribution. We found no difference in soil depth between *Trillium* and the background distribution of soil depth within the plot. Accounting for spatial covariance in soil depth ANOVAs improved the model (likelihood ratio test comparing model with and without spatial structure indicates that including spatial covariance significantly improves the model fit:  $\chi^2 = 43.607$ ,  $P < 0.001$ ). The semivariogram of soil depth reveals highly localized spatial dependence (range of spatial dependence is 1.72 m) and relatively weak spatial structure that accounts for just 23.1% of the semivariance (Fig. 3).

The three focal species also differed in proximity to neighboring trees (Fig. 2B; ANOVA:  $F_{2,764} = 27.870$ ,  $P < 0.001$ ). *Anemone* occurred in closer proximity to neighboring trees, with an average distance to the nearest tree of  $1.22 \pm 0.08$  m (SE), than either *Sanguinaria* ( $1.77 \pm 0.09$  m) or *Trillium* ( $1.91 \pm 0.05$  m). In our plot, 81% of individuals of *Anemone* were located within 2 m of a tree, compared to just 61% for *Sanguinaria* and 56% for *Trillium*. There was no significant difference between *Sanguinaria* and *Trillium* in distance to the nearest tree. These patterns varied with the size of neighboring trees (Appendix S5). *Anemone* occurred in closer proximity to large trees ( $>25$  cm DBH; mean distance to nearest large tree of  $2.10 \pm 0.14$  m) than small trees ( $<25$  cm DBH;  $3.13 \pm 0.14$  m). *Trillium* also occurred closer to large trees ( $2.93 \pm 0.09$  m) than small trees ( $3.74 \pm 0.09$  m). *Sanguinaria* did



**FIGURE 3.** Semivariogram illustrating how the strength of spatial dependence in soil depth varies across spatial scales within the study plot at McGilvra Woods State Natural Area (Sauk County, Wisconsin, USA). Points represent empirical estimates of semivariance quantifying the observed strength of spatial dependence in soil depth versus the distance between samples. The line represents the predicted semivariance from an exponential model. Text describes the estimated nugget (variation in soil depth that cannot be explained by spatial dependence), partial sill (difference between sill and nugget, the amount of variance in soil depth that can be explained by spatial dependence), and range (distance at which points may be considered independent) for the semivariogram model.

not differ in its distance from the nearest large ( $3.02 \pm 0.17$  m) and small trees ( $2.99 \pm 0.17$  m). Soil depth increased with distance from the nearest tree within the plot ( $r = 0.44$ ,  $P < 0.001$ ), although proximity to neighboring trees explained only 19.4% of the variance in soil depth (Appendix S6).

In our analysis of spatial point patterns, all three focal species exhibited conspecific aggregation at fine spatial scales within 2 m (Fig. 4A–C). The probability of observing a conspecific individual within 2 m of a given focal individual were far greater than would be expected if plants were distributed randomly in space. Additionally, each focal species tended to form clusters distributed regularly at larger spatial scales leading to a lower probability of observing conspecific pairs beyond 8 m than would be expected if plants were randomly distributed. *Anemone* exhibited particularly strong spatial clustering within 2 m and consistent segregation beyond 4 m. In general, heterospecific individuals occurred at random with respect to one another at small distances ( $<2$  m) but exhibited spatial segregation at distances greater than  $\sim 3$  m (Fig. 3E–G). *Anemone* and *Trillium* were more likely to co-occur within 0.5 m than would be expected if species were distributed at random with respect to one another, but interspecific pairs otherwise co-occurred at random within 2 m. At distances greater than 3 m, all three focal species co-occurred less often than expected from spatially random distributions reflecting the tendency for species to form conspecific clumps. *Trillium* and *Sanguinaria* occurred at random with respect to one another within 2 m but were spatially segregated at distances greater than 2 m (Fig. 3F). Our spatial analysis further illustrated clear differences in the distribution of focal species in relation to trees. *Anemone* occurred more frequently near the base of trees (within 1 m) than would be expected if plants were distributed randomly in space (Fig. 3G; Appendix S7). Meanwhile, *Sanguinaria* and *Trillium* occurred essentially at random with respect to trees in the plot (Fig. 3H, I).

## DISCUSSION

Our study documented differences in the local spatial distribution of three herbaceous plant species common to North American temperate forests that were consistent with fine-scale spatial niche partitioning and with morphological/physiological differences among those species. The local distribution of *Anemone acutiloba*, *Sanguinaria canadensis*, and *Trillium flexipes* reflected variation in soil depth and proximity to neighboring trees. *Anemone* occupied shallower soils and was found in closer proximity to trees than *Sanguinaria* or *Trillium*. These differential responses to environmental variation resulted in spatial segregation among species, an important prerequisite for environmental heterogeneity to facilitate local coexistence (Chesson, 2000a; Amarasekare, 2003). Moreover, the microsites occupied by each focal species were consistent with our predictions based on interspecific differences in plant stature, nutrient requirements, and accompanying physiological traits suggesting local species-environment distributions result from environmental sorting and competition.

*Anemone*—a short-statured evergreen species with low photosynthetic rates, low nutrient demands, and a shallow root system—occurred more commonly in microsites with shallow soils and near canopy trees. Evergreen herbs in temperate forests generally place their leaves close to ground level, possibly to enhance leaf temperature and photosynthesis in fall and spring when other herbs are below ground, but such short stature puts them at a competitive

disadvantage on moister, more fertile microsites that support dense herb coverage in midsummer (Givnish, 1982, 1987).

Meanwhile, *Sanguinaria* and *Trillium*—relatively tall-statured early summer species with higher photosynthetic rates, greater nutrient demands, and more substantive root systems—were distributed across a broader range of soil depths and did not cluster near canopy trees. Such species presumably are excluded from such microsites not by competition with *Anemone* but by physiological intolerance, given that their greater moisture and nutrient demands are unlikely to be met on thin soils, and the costs of building tall stems would remain high while the photosynthetic benefits would be low (Givnish, 1982). Both *Anemone* and *Trillium* were found closer to large trees than small trees. This pattern could reflect biologically relevant environmental differences in microsites surrounding trees of varying sizes, or a sampling effect caused by the increased time for herbs to colonize and spread near large trees.

Although previous research has demonstrated how spatial environmental heterogeneity influences local herb distributions within temperate forests (Struik and Curtis, 1962; Bratton, 1976; Hicks, 1980; Beatty, 1984, 2014; Crozier and Boerner, 1984; Vellend et al., 2000; Frelich et al., 2003; Burton et al., 2011; McIntosh et al., 2016), our study expands on this previous work by linking local distributions to interspecific differences in leaf phenology, leaf stature, leaf nutrient concentrations and rooting depth. Bratton (1976) previously argued that rooting depth constrained the distribution of herbaceous species with more substantial belowground organs to deeper soils, while herbs with fibrous roots and small rhizomes were more commonly found in shallow soil microsites near the base of trees, boulders, or exposed rocky substrate.

The distributions of *Anemone*, *Sanguinaria*, and *Trillium* are consistent with Bratton's argument based on root depth alone. But several other morphological, physiological, and phenological differences among species accompany this variation in rooting depth (Givnish, 1987, 2002; Uemura, 1994; Neufeld and Young, 2014). Sparse cover on shallow soils should favor short-statured herbs based on game-theoretic considerations (Givnish, 1982, 1995). Shallow and/or infertile soils favor evergreen vs. deciduous plants (Givnish, 2002), and evergreens with long-lived leaves have photosynthetic rates and lower N concentrations per unit leaf mass (Reich et al., 1997; Givnish, 2002).

Evergreen herbs should place their leaves at or near ground level to enhance photosynthesis in late fall and early spring, but such low leaf height should place them at a competitive disadvantage on moister, more fertile microsites that support more herb coverage in midsummer (Givnish, 1982, 1995). Evergreen herbs, which renew their foliar nutrients less frequently, should allocate less to roots than deciduous herbs in the same temperate forest understory. Indeed, evergreen herbs like *Anemone* often have shallow rooting systems, shorter stature, lower photosynthetic rates, and lower nutrient demands (Givnish, 1987). Evergreen herbs have longer periods over which to amortize the costs of leaf production and should thus, often have an advantage on nutrient-poor or densely shaded sites (Givnish, 2002). Photosynthetic activity during cool periods in fall and spring may be also be correlated with narrow xylem conduits that resist cavitation because of late frosts, but have low conductance and may be unable to support the high transpiration rates associated with more productive, later leafers (see Givnish, 2002 and Lopez et al., 2008 for these arguments applied to canopy trees).

Furthermore, soil depth is just one of several environmental factors that vary with distance from tree bases and influence plant

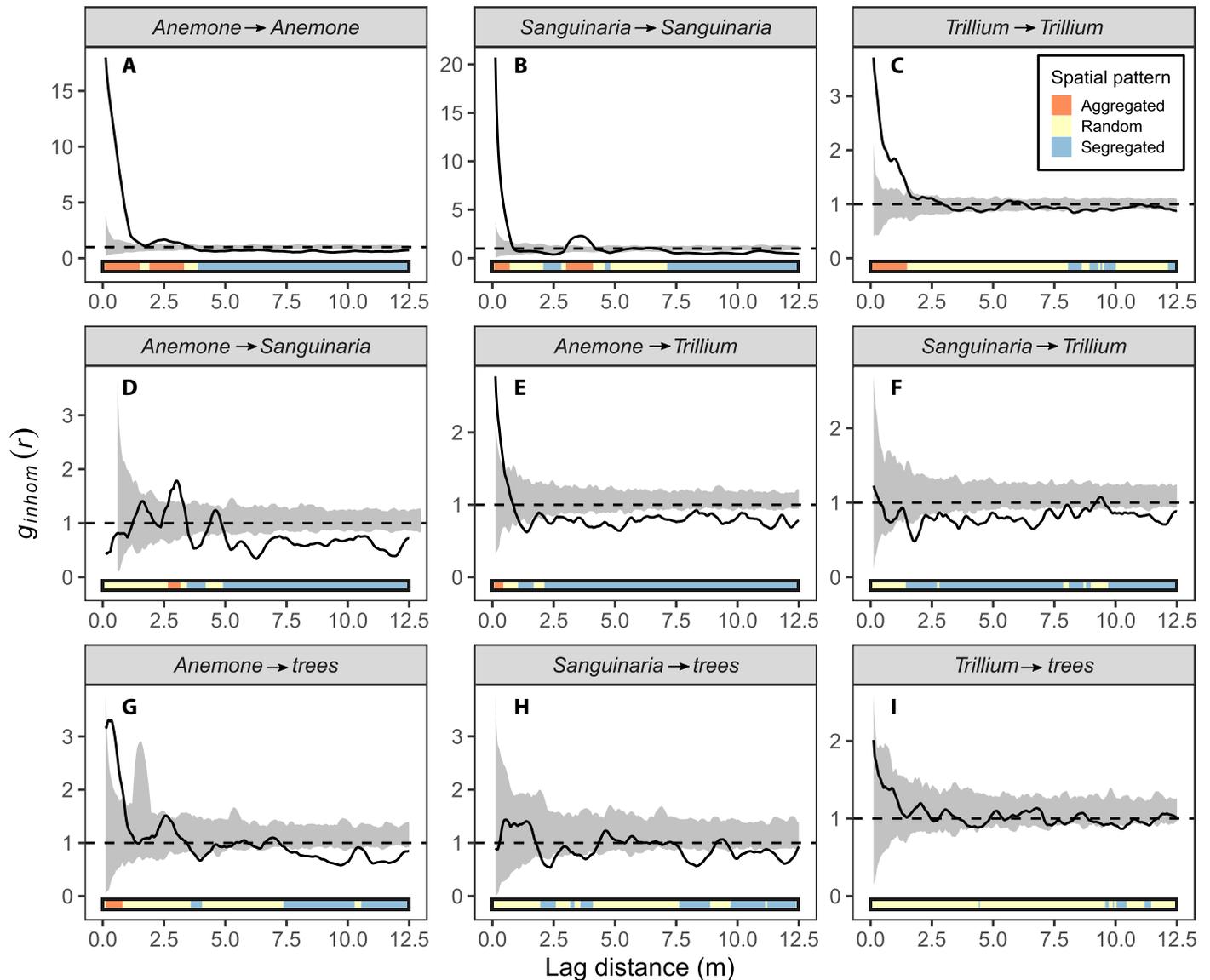
growth and competition. The distribution of *Anemone*, *Sanguinaria*, and *Trillium* are consistent with these predictions. However, other physiological differences accompany this variation in rooting depth (Givnish, 1987; Uemura, 1994; Neufeld and Young, 2014).

Evergreen herbs like *Anemone* often have shallow rooting systems, shorter stature, lower photosynthetic rates, and lower nutrient demands (Givnish, 1987), and can require less midsummer light to break even energetically than deciduous herbs (Givnish, 2002). Furthermore, soil depth is just one of several environmental factors that influences plant growth and competition near the base of trees. These microsites are likely to be low on supplies of light, water, and nutrients because of tree bole cutting off the light from half the sky in summer, and shallow rooting zones favoring shorter herbs with longer photosynthetic seasons. These microsites may sometimes also be nutrient-poor per unit soil volume as a result of stemflow leaching nutrients or washing away fine particles that are important for retaining soil nutrients and moisture (Levia and Frost, 2003; Barbier et al., 2008). In some cases, however, nutrients brought by stemflow vs. throughflow can enrich soil fertility per unit volume near tree boles, perhaps based on bark texture or chemistry, or substrate chemistry. For example, Andersson (1991) found greater concentrations of Ca and S near tree boles in a Swedish *Quercus robur* forest over a rich clayey soil.

In an Ohio mesic forest, Boerner and Koslowsky (1989) documented higher rates of  $\text{NH}_4^+$  mineralization near *Acer saccharum* boles than around those of *Fagus grandifolia* or *Fraxinus americana*, or on microsites >2 m away from any tree bole. On the other hand, stemflow concentration of P in *Acer saccharum* was less than one-third that for *Fagus grandifolia* in another forest in northern New York (Zhang and Mitchell, 1995). Reviewing several additional publications (e.g., Gersper and Holowaychuk, 1971; Eaton et al., 1973; Rolfe et al., 1978), we found no clear pattern toward soil impoverishment or enrichment per unit volume at the base of sugar maple trees.

Early snowmelt and the formation of thaw circles may affect plant distributions by extending the growing season near the base of trees (Veblen et al., 1977; Vellend et al., 2017). As dark tree boles absorb sunlight in early spring, radiant heat melts snow and accelerates soil thaw near the tree base. The additional days of unobstructed light and access to belowground water should provide an important energetic boost for evergreen plants growing near the bases of trees, such as *Anemone* growing near the base of trees. Spring ephemerals could similarly benefit from an extended photosynthetic season (Vellend et al., 2017), although they have greater nutrient demands than evergreen herbs and may be inhibited by small soil volumes, leaching, or dry soils near tree boles.

In contrast, early thaw should have less influence on early summer species such as *Sanguinaria* and *Trillium* whose leaves emerge later in the spring. The greater height of *Sanguinaria* and *Trillium*, however, should be advantageous in microsites with greater herb coverage on deeper soils farther from tree bases, where they competitively exclude short evergreen species with low rates of photosynthesis (see Givnish, 1982, 1987, 1995, and the introduction to this paper). Shorter, shallowly rooting evergreens should be better able to tolerate thin soils near tree boles, and such microsites might become refuges from taller competitors. Other relatively small-statured plants with insubstantial root systems that exhibit a similar distribution to *A. acutiloba* include *Mitella diphylla* (J. Beck, personal observation), *Micranthes virginianensis* (T. Givnish, personal observation), and *Sedum ternatum* (Bratton, 1976). *Sedum* is evergreen,



**FIGURE 4.** Pair correlation functions describing how the probability of observing a focal individual varied with proximity to conspecific individuals (A–C), heterospecific individuals for each pair of focal species (D–F), and neighboring trees (G–I). The black line illustrates how the observed pair correlation function,  $g_{\text{inhom}}(r)$ , varies with distance while the gray ribbon represents a simulation envelope for  $g_{\text{inhom}}(r)$  under complete spatial randomness. Aggregated spatial patterns occur when the probability of occurrence exceeds that expected under spatial randomness while segregated patterns occur when the probability of occurrence falls below that expected under complete spatial randomness.

while *Micranthes* and *Mitella* have shorter-lived deciduous leaves. Physiological integration among rooting depth, leaf height, nutrient requirements, plant hydraulics, and photosynthetic phenology coupled with covariance among multiple environmental factors makes it difficult to disentangle which factors actually constrain local herb distributions in any observational study (Givnish, 1982, 1987, 1995; Uemura, 1994; Lapointe, 2001; Rothstein and Zak, 2001; Neufeld and Young, 2014), but the parallel trends expected in plant traits driven by parallel trends in environmental factors may make this point moot.

The tendency of our focal species to cluster spatially likely reflects, at least in part, patterns of seed dispersal, and possibly unmeasured environmental variables or vegetative spread beyond the threshold we used to delineate individuals. All three species exhibited conspecific aggregation within  $\sim 2$  m (Fig. 3A–C). Given

that soil depth within the plot exhibited relatively weak spatial structure, patterns of seed dispersal likely contribute to conspecific spatial aggregation. All three focal species possess elaisomes and are primarily dispersed by a suite of generalist ant species (Pudlo et al., 1980; Handel et al., 1981; Smith et al., 1989). Dispersal in myrmecorous species tends to occur at relatively short distances, often  $< 1$  m (Smith et al., 1989; Kalisz et al., 1999). Limited dispersal likely reinforces fine-scale conspecific aggregation and the tendency for species to segregate and form regularly spaced clumps at coarser scales. Notably, the observed scale of spatial dependence in soil depth (1.72 m; Fig. 3), the spatial scale of intraspecific aggregation (0.75–1.59 m; Fig. 4), and expected dispersal distances (1–2 m) all align closely in our study. More extensive dispersal has the potential to undermine the stabilizing effects of environmental heterogeneity

on species coexistence if rates of dispersal outpace the competitive interactions that sort species according to local environmental variation (Leibold et al., 2004; Snyder and Chesson, 2004). The spatial segregation among focal species beyond 2 m and environmental distributions are consistent with our predictions and provide evidence of local spatial niche partitioning.

Niche-based processes predicated on environmental heterogeneity and spatial resource partitioning are often invoked to explain local patterns of species diversity in temperate forests and many other plant communities (Chesson, 2000b; Amarasekare, 2003; Silvertown, 2004; HilleRisLambers et al., 2012; Stein et al., 2014). Nevertheless, the potential for fine-scale environmental heterogeneity depends on (1) the scale of environmental heterogeneity relative to dispersal capacity and (2) whether physiological tradeoffs are sufficiently strong to maintain local species-environment associations (Lundholm, 2009; Tamme et al., 2010; Beatty, 2014). This study illustrates the importance of characterizing the spatial structure of environmental variations and empirical patterns of aggregation and segregation in relation to dispersal capacity. Such observations are critical for assessing the potential for environmental heterogeneity to drive fine-scale spatial niche partitioning in plant communities. We show that local species-environment relationships are predictable based on morphological, physiological, and phenological characteristics and that heterospecific individuals remain spatially segregated as environmental sorting, competition, and dispersal play out at local scales. This study advances our understanding of how environmental heterogeneity could maintain high local plant diversity in temperate forest understories (Bratton, 1976; Beatty, 1984, 2014; Vellend et al., 2000; Peet et al., 2014; Catella et al., 2019), the spatial scale at which forest herbs can partition habitat (Amarasekare, 2003; Hart et al., 2017), and, more generally points to the importance of spatial resource partitioning in promoting local plant diversity (Amarasekare, 2003; Silvertown, 2004; Lundholm, 2009; Bartels and Chen, 2010; Stein et al., 2014).

## ACKNOWLEDGMENTS

The authors thank B. Bowser, R. Nelson, K. Hobbins, and C. Viellieux for assistance with data collection. The Wisconsin Department of Natural Resources, especially T. Meyer and N. Fayram, provided logistical support. In addition, M. Persche provided illustrations of the focal species; D. Waller, A. Ives, M. Turner, B. Larget, J. Richards, and A. Salvi offered constructive feedback. We also thank two anonymous reviewers for helpful comments that improved the manuscript.

## AUTHOR CONTRIBUTIONS

T.J.G. conceived the theoretical foundation for this study. J.J.B. designed the study, conducted the fieldwork, and analyzed the data. J.J.B. and T.J.G. wrote the manuscript.

## FUNDING INFORMATION

This research was supported by a Davis Grant from the UW-Madison Botany Department and a Graduate Research Fellowship from the UW-Madison Arboretum to J.J.B. J.J.B. was supported as

an NSF Graduate Research Fellow (DGE-1747503). T.J.G. was supported by NSF grant DEB-1557096. Opinions, findings, and conclusions expressed here are those of the authors and do not reflect the views of the NSF. Support was also provided by the Graduate School and the Office of the Vice Chancellor for Research and Graduate Education at the University of Wisconsin-Madison with funding from the Wisconsin Alumni Research Foundation.

## DATA AVAILABILITY

Data and metadata used in this paper can be found in Appendices S8–S11. See Appendix 12 for a script with R code used to analyze these data.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**APPENDIX S1.** Map illustrating the location of the study site, McGilvra Woods State Natural Area (Sauk County, Wisconsin, USA) and photographs of *Anemone acutiloba*, *Sanguinaria canadensis*, and *Trillium flexipes*.

**APPENDIX S2.** Summary of tree composition within the 50 × 50 m study plot.

**APPENDIX S3.** Histogram of leaf nitrogen content for 242 understory forest herbs.

**APPENDIX S4.** Map of tree distributions within the 1 ha forest monitoring plot at McGilvra Woods State Natural Area.

**APPENDIX S5.** Influence of tree size on herb spatial patterns.

**APPENDIX S6.** Scatterplot illustrating the relationship between proximity to trees and soil depth within the study plot at McGilvra Woods State Natural Area.

**APPENDIX S7.** Photograph illustrating the tendency for *Anemone acutiloba* to cluster near the base of large trees.

**APPENDIX S8.** Metadata for fine-scale environmental heterogeneity and spatial niche partitioning among spring-flowering forest herbs.

**APPENDIX S9.** Herb distribution data within the study plot at McGilvra Woods State Natural Area.

**APPENDIX S10.** Soil depth data within the study plot at McGilvra Woods State Natural Area.

**APPENDIX S11.** Herb distribution data within the study plot at McGilvra Woods State Natural Area.

**APPENDIX S12.** R script used to analyze data.

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