

Demography, Time to First Flowering and Longevity of 14 Temperate Forest Herbaceous Species, Iowa, USA

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ABSTRACT

The ability of temperate forest herbaceous species to recover from anthropogenic disturbance and to colonize new secondary woods is limited by both seed shortage (lack of dispersal) and suitable safe sites (sites where seedling establishment is possible). In this study, which originated in 1998–99, I added seeds of 14 species, including six phylogenetically related pairs classified as common or restricted in distribution, to both occupied and unoccupied upland forest sites. I recorded emergence the first year and followed yearly survival for an additional five years. Adding seeds resulted in flowering individuals for 12 of the 14 species and an additional species established by vegetative spread. I concluded that dispersal, rather than safe sites, was most limiting. Species with restricted distributions, which also have larger seeds than related common species, had higher survivorship over five years. Minimum longevity ranged from 8–18 years, suggesting that once on site, long-term persistence is possible. A practical implication of these results is that limited funding and other resources can be focused on seed addition techniques, particularly for larger-seeded species. Because the mean age to first flowering was six years, a second practical implication is that the traditional monitoring protocol of following plants through to reproduction as a measure of restoration success may be difficult for many long-lived species. Using “citizen scientists” to monitor may help make long-term monitoring more feasible beyond the limited time frame of grant funding.

Keywords: first flowering, forest herbaceous species, longevity, safe sites, seed limitation

Restoration Recap

- The ability of temperate forest herbaceous species to recover from disturbance, expand existing populations and to colonize new secondary woods may be limited by both seed shortage (lack of dispersal) and suitable safe sites (sites where seedling establishment is possible). This study demonstrated seed limitation, as 13 of 14 species included in the study successfully established at both occupied and unoccupied sites.
- The long time to first flowering suggests restoration of these species through seed addition requires patience; however, their long lifespans also suggest that, once established, lengthy population persistence is possible.

Anthropogenic disturbances in the Midwest and eastern United States are widespread and include conversion of forests to agriculture, domestic animal grazing, deer overpopulation and timber harvest (Roberts and Gilliam 2014). The ability of temperate forest herbaceous species to recover from these disturbances, and to colonize new secondary woods can be limited by both insufficient seed

arriving on-site, and/or lack of suitable sites for seedling establishment (Eriksson and Ehrlén 1992).

Seed limitation or lack of dispersal may be due to low reproductive output, heavy seeds that are not dispersible, lack of structures to aid long distance dispersal, and short dormancy (Fröborg and Eriksson 1997, Verheyen et al. 2003, Mabry 2004, Flynn and Vellend 2005, Gilliam 2007). Seed limitation can be determined by introducing seed and monitoring emergence and survival. If seeds are limiting colonization, introducing seeds will result in new populations that survive and reproduce (Ehrlén and Eriksson 2000, Menges 2008) and, ideally, result in second and later generation of individuals (Menges 2008).

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Factors that may limit suitability of sites for seedling include environmental factors such as light, pH or soil moisture (Jules 1998, Petersen and Philip 2001, Vellend 2005), as well as biological factors, including competition, herbivory, shade, seed predation and especially litter (Rust and Roth 1981, Reader 1993, Eriksson 1995, Fröberg and Eriksson 1997, Ehrlén and Eriksson 2000).

Seed limitation may be especially important for species that are restricted in distribution (due to a narrow geographic range or because they occur in small populations throughout their range). These species often have larger seeds than related common species and, because there is a tradeoff between seed size and number, these species also produce fewer seeds, further limiting seed availability (Jacobsson and Eriksson 2002, Murray et al. 2002, Mabry 2004 and references therein). Conversely, smaller seeded species have an “output advantage”, where any one seed is more likely to reach a suitable safe site compared to a species with lower seed output (Jacobsson and Eriksson 2002).

Whether seeds or safe sites are limiting is particularly important in developing restoration strategies because the strategy will vary according to which factor is more limiting. If the major bottleneck is lack of seeds and seed dispersal, restoration efforts can be focused on simply introducing seeds to restoration sites (Vellend 2005). However, if availability of suitable safe sites is the limiting factor, much more effort will need to be focused on understanding safe site requirements and identifying or preparing suitable safe sites (Dobson et al. 1997, Vellend 2005).

This study originated in 1998–1999 and addressed whether seeds are limiting the establishment of new populations, and, if seeds are limiting, whether common species and species with a more restricted distribution differ in their degree of seed limitation. Due to subsequent long-term monitoring, I was also able to document the mean time to first flowering for each species, the percent of individuals that emerged that went on to flower, and minimum longevity. Flowering provides evidence for the potential establishment of a new population (Turnbull et al. 2000).

Methods

Based on a previous floristic inventory of 103 permanently marked plots in central Iowa, U.S.A. forests, 12 species were selected and assigned as common or restricted based on frequency of occurrence (number of plots where a species was present) (Mabry 2000). None of the less common species chosen would qualify for inclusion as a state threatened and endangered species; therefore, I chose the term restricted in distribution to describe the less abundant species. Restricted in this article refers to the frequency of a species (i.e., the percent of plots in which each species occurred) relative to the closely related common species (Table 1). Specifically, common refers to species that occurred in at least 50% of plots, and restricted species

were from 34% to 90% less frequent than the species to which they were compared. The exception to this was the pairing of *Viola sororia* (dooryard violet) and *Viola pubescens* (downy yellow violet). *V. pubescens* was only 21% less frequent than *V. sororia*, but was strongly associated with the highest quality, least disturbed woods in the study area (Mabry 2002). An additional two species, not paired by common vs. restricted, were also included in the study, for a total of 14 species (Table 1).

An additional criterion for species selection was the ability to match common and restricted species within genus or family. Although species within each pair may differ in some significant ways, each pair shares far more affinities with one another than with the members of the other pairs, particularly in fruit and seed morphology, and in dispersal mode. The purpose of this pairing was to avoid potentially confounding these important traits among common and restricted species. Robust phylogenies for many major plant groups are not available (Gaston 1994); however, comparing congeneric or confamilial pairs of species is an acceptable substitute because we can be reasonably sure that these pairs share a more recent common ancestor than species from other genera or families (Silvertown and Dodd 1997).

I collected seeds upon ripening in the same year that they were sowed and were stored dry if the seeds tolerate dry storage, or refrigerated in moist sphagnum if they do not (Cullina 2000). Seeds were planted between July and November 1998 and between May and December 1999.

I planted seeds of the species pairs in both occupied and unoccupied sites. Occupied sites were chosen based on whether the site had existing populations of each species. These were forest preserves (state and country parks) with little historical human disturbance, and that had not been grazed or harvested for at least 50 years at the time the study was initiated. Unoccupied sites did not have existing populations of the species pairs. They included two 50-year-old secondary woods (one was subsequently burned and lost as a study site) and a formerly pastured woods that is now a state preserve. All sites were largely free of non-native species that commonly invade forests and woodlands in this area, such as *Bromus inermis* (smooth brome), *Alliaria petiolata* (garlic mustard), *Lonicera* spp. (honeysuckle), and *Rhamnus cathartica* (buckthorn). The sites were all representative of central Iowa closed canopy upland hardwood forests, with an overstory dominated by *Quercus alba* (white oak), *Quercus macrocarpa* (bur oak), *Quercus rubra* (red oak), *Quercus velutina* (black oak), *Carya ovata* (shagbark hickory), *Acer nigrum* (black maple), *Tilia americana* (American linden) and *Prunus serotina* (black cherry) (van der Linden and Farrar 2011). I did not attempt to match species to specific microenvironmental factors. Phenotypic plasticity is ubiquitous among plants in general (Sultan 1987), including among shade tolerant herbaceous species of this region (Altrichter

Table 1. Fourteen Iowa woodland understory species in seven families studied for seedling emergence and survival in occupied and unoccupied sites. Status refers to common species (C) vs. restricted (R); sites are the number of forested sites planted for each pair; numbers in parentheses are the number of plots per site. Each plot included two subsamples of 15 seeds of each species planted in an alternating grid.

Family and Species	Frequency (% of 103 Plots)	Status	Occupied Sites	Unoccupied Sites
Asteraceae				
<i>Solidago ulmifolia</i>	53.4	C	2 (2)	2 (2)
<i>Solidago flexicaulis</i>	30.1	R	2 (2)	2 (2)
Berberidaceae				
<i>Podophyllum peltatum</i>	57.3	C	3 (3)	2 (2)
<i>Caullophyllum thalictroides</i>	11.7	R	3 (3)	2 (2)
Cyperaceae				
<i>Carex blanda</i>	90.3	C	3 (3)	2 (2)
<i>Carex jamesii</i>	47.6	R	3 (3)	2 (2)
Liliaceae				
<i>Erythronium albidum</i>	67.0	C	3 (3)	2 (2)
<i>Uvularia grandiflora</i>	35.0	R	3 (3)	2 (2)
Poaceae				
<i>Festuca obtusa</i>	84.5	C	2 (2)	2 (2)
<i>Elymus villosus</i>	8.7	R	2 (2)	2 (2)
Ranunculaceae				
<i>Hepatica acutiloba</i>	14.6	NA	2 (2)	2 (2)
<i>Isopyrum bitematum</i>	18.5	NA	2 (2)	2 (2)
Violaceae				
<i>Viola sororia</i>	95.2	C	2 (2)	2 (2)
<i>Viola pubescens</i>	74.8	R	2 (2)	2 (2)

et al. 2020). Plasticity gives plants the ability to adjust to heterogeneity in environmental factors such as light and soil moisture (Sultan 1987). For example, in a classic paper, Bray (1957) noted numerous instances where “climax” forest herbs were found growing prairies in the Midwest.

I planted three species pairs in three occupied sites the first year of the study (1998), with three plots per site. In 1999 four additional species pairs were added to occupied sites and all seven species pairs to unoccupied sites. Due to time constraints 1999, planting was reduced two sites per pair, with two plots per site. Table 1 gives a complete list of species and families, frequency of occurrence, and the number of sites and replicates included for each species.

Each plot had two subplots that were each made up of a grid of 30 seeds (15 seeds of each species). The grids were arranged in a pattern of five rows with six seeds/row, with the position of species alternating on each row, so that the seeds of each species were intermixed. Across all species I planted a total of 4,380 seeds (Table S1).

Prior to planting litter was removed and the existing vegetation was gently pushed aside. Seeds were planted

0.5–1.0 mm below the surface, depending on seed size. After planting, the soil directly above the seed was gently compacted and the litter was replaced. Otherwise, there was no disturbance or additional site preparation. Because seeds in this study were planted and not simply sowed on the soil surface, this study did not include the possibility that seeds may arrive at a site but do not receive sufficient contact with soil to germinate.

Seeds were planted 10 cm apart, and each seed was marked by a small plastic straw so that it could be relocated the following spring. In the first spring the straws were relocated and the seeds were scored for emergence at a minimum of one-week intervals. When no new seeds emerged for two successive intervals, scoring was concluded for that year. The seedlings were then marked and monitored each year until they died or reached reproductive maturity (considered a measure of new population establishment). The standard protocol when adding seed is to then follow individuals through fruit set and production of new seedlings (Menges 2008) or at least up to reproductive maturity (Turnbull et al. 2000).

Table 2. Mean and SD of percent emergence and survival over five years for six common and restricted species, and results of two-way ANOVA. The data were log transformed before analysis. Effect size is considered moderate when the calculated Cohen's d is above 0.500.

Status	Percent (SD)	Mean Square	F-ratio	P-value	Cohen's d
Emergence					
Mean Common	23.5 (18.4)	0.009	0.12	0.728	0.414
Mean Restricted	33 (27.9)				
Survival year 1					
Mean Common	8.3 (10.3)	0.388	3.79	0.055	0.586
Mean Restricted	15.2 (14.8)				
Survival year 2					
Mean Common	8.4 (10.3)	0.216	2.06	0.156	0.508
Mean Restricted	14.6 (14.2)				
Survival year 3					
Mean Common	7.7 (9.8)	0.54	4.75	0.039	0.530
Mean Restricted	13.9 (13.5)				
Survival year 4					
Mean Common	7.4 (9.5)	0.53	4.89	0.031	0.431
Mean Restricted	12.2 (12.6)				
Survival year 5					
Mean Common	5.5 (5.5)	0.763	9.37	0.003	0.521
Mean Restricted	10.4 (11.6)				

In the last year of monitoring (2018) only eight individuals had not yet died or flowered: three *Caulophyllum thalictroides* (blue cohosh), three *Podophyllum peltatum* (Mayapple), one *Erythronium albidum* (trout lily), and one *Solidago flexicaulis* (zig-zag goldenrod). This long-term monitoring of survival also allowed me to measure mean time to first flowering and the percent of individuals that emerged and went on to flower. It also allowed me to estimate minimum longevity for each species. Minimum longevity was based on the number of years that I could track individual marked plants until they could no longer be distinguished from new individuals that occurred due to self-sowing or vegetative spread.

Survival data beyond five years is not presented here because by year six surviving plants in *Asteraceae*, *Cyperaceae*, *Poaceae*, *Ranunculaceae* and *Violaceae* were self-sowing or spreading vegetatively, and I could no longer distinguish these new individuals from those that were originally planted. Instead, long-term population trends will be modelled (Harmes and Mabry, *in prep*).

To gain insight into how differences in viability might help explain subsequent differences in emergence rates, I also tested for seed viability. Although seeds for viability would ideally be from the same lot as seeds used in the planting study, this was not possible due to time constraints. Seeds were collected from a subset of the sites where I planted seeds.

This leaves open the possibility that there was year to year variation in viability and that the tested seeds are not representative of the planted seeds. However, the most common environmental factors that influence seed germinability include day length, and amount and quality of light (Guterman 2000), factors that would not have varied between 1998–99 (seed planting) and 1999–2000 (seed testing).

In 1999–2000 I collected seeds for each species from three sites, with the species pairs collected from the same sites. At each site, two samples per species were collected, for a total of six replicates. Each sample consisted of 25 seeds. Seeds were tested for viability by slicing imbibed seeds to expose the embryo, then placing seeds on a 1.0% solution of 2,3,5 triphenyl-24-tetrazolium chloride (TZ). TZ reacts with respiring tissue to turn it pink, thus indicating viability.

Emergence and survival of 12 of 14 species pairs were analyzed using two-way ANOVA, where common vs. restricted was the independent variable, and emergence and survival the dependent variables. Family was treated as a block because I wanted to control for variation among families, but these results were not presented as I was not interested in this source of variation as an experimental question. The experimental unit was plots within sites for the emergence and survival data. *Isopyrum biterminalum* (false rue anemone) and *Hepatica acutiloba* (sharp-lobed

Table 3. Mean number of years to first flowering, percent flowering (numbers in parentheses are numbers of individuals that emerged that went on to flower), and number of sites with flowering individuals (numbers in parentheses are number of sites where seeds were sown). Status refers to C=common, R=restricted.

Family	Status	Species	Mean Years to First Flowering	Percent Flowering	Minimum Longevity	Number of Sites Established
Asteraceae	C	<i>Solidago ulmifolia</i>	NA	0.0 (0)	12	0(4)
	R	<i>Solidago flexicaulis</i>	8.0	6.7 (3)	10	2(4)**
Berberidaceae	C	<i>Podophyllum peltatum</i>	18*	0.8 (1)	18	2(5)**
	R	<i>Caulophyllum thalictroides</i>	10.1	9.4 (8)	18	3(5)
Cyperaceae	C	<i>Carex blanda</i>	3.2	8.9 (5)	15	2(5)
	R	<i>Carex jamesii</i>	7.5	34.1 (14)	15	3(5)
Liliaceae	C	<i>Erythronium albidum</i>	NA	0.0 (0)	18	1(5)**
	R	<i>Uvularia grandiflora</i>	12.0	6.2 (6)	18	3(5)
Poaceae	C	<i>Festuca obtusa</i>	3.3	20.3 (24)	8	3(4)
	R	<i>Elymus villosus</i>	3.9	12.9 (27)	8	4(4)
Ranunculaceae	NA	<i>Hepatica acutiloba</i>	5.1	14.1 (9)	10	2(4)
	NA	<i>Isopyrum binternatum</i>	5.0	5.0 (5)	10	2(4)
Violaceae	C	<i>Viola sororia</i>	4.0	3.5 (11)	8	1(4)
	R	<i>Viola pubescens</i>	3.9	31.9 (30)	10	4(4)
Mean			6.0	11.0	12.7	

* Only one individual flowered and is not included in the mean.

** One population established vegetatively.

hepatica) were planted identically but were not included in the analysis because, while they had a low frequency of occurrence in the sample plots (Table 3), I did not have a congeneric common species to pair them with.

Because it is possible to obtain statistically significant results, but with low effect size (Nuzzo 2014), I also calculated Cohen's d effect size for the differences between common and sparse species. Cohen's d = mean group 1 – mean group 2/SD. The pooled SD was adjusted for differences in sample size. Effect size is considered medium when Cohen's d is above 0.500, and large when it is above 0.800 (Lenhard and Lenhard 2016).

Results

Species with restricted distributions had greater percent emergence and higher survival in each of the subsequent five years (Table 2). Although these differences were not detected statistically until year three of survival, Cohen's d effect sizes were either on the border between slight and moderate effect, or of moderate effect (Lenhard and Lenhard 2016; Table 2). Mean viability was similar for common and restricted species, 84.0 (SD=13.2) versus 77.5 (SD=20.7).

For the 78 individuals where I could determine cause of mortality, 42 instances were due to browsing, 17 due to trampling, with the remainder due to competition with adjacent shrubs, burrows, falling branches and logs, an ATV trail, frost, and flood debris.

The mean age to first flowering ranged from 3.2 years (*Carex blanda*, white sedge) to 12.0 years (*Uvularia grandiflora*, large-flowered bellwort). One *P. peltatum* flowered after 18 years. The average age to flowering of the 14 species was seven years. When the one *P. peltatum* that flowered after 18 years was removed from the calculation, the mean number of years to flowering was six years (Table 3).

The percent of individuals that emerged and went on to flower ranged from zero (*E. albidum* and *Solidago ulmifolia*, elm leaved goldenrod) to 34.1 (*Carex jamesii*, James' sedge) (Table 3). Minimum longevity ranged from eight to 18 years (Table 3). After six years, 12 of the 14 species had flowering individuals, and one additional species (*E. albidum*) established by vegetative spread, suggesting the potential establishment of new populations (Table 3).

Discussion

Adding seeds resulted in flowering individuals for 12 of 14 temperate forest herbaceous species, and a new colony by vegetative reproduction for an additional species. I did not test safe site limitation directly; however, because seeds emerged and plants survived in both occupied and unoccupied sites, I concluded that dispersal is the greater limiting factor in the establishment of new populations of these species. This result aligns with other seed addition studies supporting seed limitation as a common barrier to colonization (Eriksson and Ehrlén 1992, Ehrlén and Eriksson 2000, Turnbull et al. 2000, Petersen and Philip 2001, Verheyen et al. 2003, Graae et al. 2004, Brudvig et al. 2011).

Restricted species in this study had higher survivorship over five years compared to the paired common species. Past work has also shown that the same restricted species included in this study have significantly larger seeds than the related common species (Mabry 2004). The higher survivorship is likely due to the greater resources large seeds have to overcome shade and to produce larger more competitive shoots (Leishman and Westoby 1994).

This supports other work that has found that, once on site, larger-seeded species are able to withstand site specific hazards, such as shade, drought, and nutrient limitation (Reader 1993, Eriksson 1995, Fröberg and Eriksson 1997, Jacobsson and Eriksson 2002), although see Graae et al. (2004). In contrast, establishment of smaller-seeded species may have been aided if I had included modest site preparation such as clearing excess litter (Eriksson 1995).

The longevity documented in this study favors persistence once on site. The minimum life span for the species included in this study ranged from eight to 18 years. These long lifespans are on par with what others have found (Bierzychudek 1982, Jolls and Whigham 2014), suggesting that low seed output noted for many long-lived forest herbaceous species (Bierzychudek 1982, Mabry 2004, Whigham 2004, Flinn and Vellund 2005) can be compensated by long and continuous reproductive effort (Rust and Roth 1981).

In 2023 I conducted an informal survey at four sites where monitored plants had flowered by 2018. I found spreading populations of *S. flexicaulis*, *C. jamesii*, *C. blanda*, *H. acutiloba*, *I. biternatum*, *V. sororia*, *V. pubescens*. I could still identify marked individuals that were flowering of *P. peltatum* and *C. thalictroides*, extending their minimum lifespan another five years, to 23 years.

Another factor favoring persistence is that many long-lived forest herbaceous species rely on vegetative reproduction (Sobey and Barkhouse 1977, Bierzychudek 1982, Mottl et al. 2006, Goodwillie and Jolls 2014). In fact, of the 14 species included in this study only *C. blanda* and *C. thalictroides* have low to no vegetative spread (Mabry and Fraterrigo 2009). Vegetative reproduction might also serve as a form of reproductive assurance in that it may

allow persistence when pollinators are unavailable and reproductive output is low (Goodwillie and Jolls 2014).

There are two practical implications for restoration from this study. First it demonstrates that restoring shade tolerant herbaceous species by seed is a feasible restoration technique in addition to transplants. Therefore, limited funding and other resources for restoration can be focused on developing sources of seeds and on planting and transplant methods, rather than the much more labor-intensive effort to understand and create suitable safe sites (Vellend 2005). Although my study did not test safe site suitability directly, the emergence and survival that I recorded would not have been observed had there not been suitable safe sites.

A second practical implication concerns protocols that specify monitoring continue through the complete plant life cycle: flowering, fruiting, dispersal, and additional seedling establishment (Menges 2008) or at least until plants reach reproductive age (Turnbull et al. 2000). Because mean age to first flowering was six years, monitoring these long-lived forest perennials is needed beyond the timeframe of most grant funding. One alternative to achieve long-term monitoring is a “citizen science” approach, where volunteer participants collect and analyze ecological data (Edwards et al. 2018). In addition, citizen science supports other goals of restoration, including education and engaging communities (Edwards et al. 2018).

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References

- Altrichter, E.A., C.M. Mabry, J.R. Thompson and R.K. Kolka. 2020. Genetic differentiation and phenotypic plasticity of forest herbaceous species in Iowa, Central United States. *Ecological Restoration* 38:160–168.
- Bray, J.R. 1957. Climax forest herbs in prairie. *The American Midland Naturalist* 58:434–440.
- Bierzychudek P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: A review. *New Phytologist* 90: 757–776.
- Brudvig, L.A., C.M. Mabry and L.M. Mottl. 2011. Dispersal, not understory light competition, limits restoration of Iowa woodland understory herbs. *Restoration Ecology* 19:24–31.
- Cullina, W. 2000. *Growing and Propagating Wildflowers of the United States and Canada*. Boston, MA: Houghton Mifflin Company.
- Dobson, A.P., A.D. Bradshaw and J.M. Baker. 1997. Hope for the future: Restoration ecology and conservation biology. *Science* 277:515–522.

- Edwards, P.M., G. Shaloun and D. Bedell. 2018. A unique role for citizen science in ecological restoration: A case study in streams. *Restoration Ecology* 26:29–35.
- Ehrlén J. and O. Eriksson. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81:1667–1674.
- Eriksson, O. 1995. Seedling recruitment in deciduous forest herbs: The effects of litter, soil chemistry and seed bank. *Flora* 190: 65–70.
- Eriksson, O. and J. Ehrlén. 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91:360–364.
- Flinn, K. and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment* 3:343–350.
- Fröberg, H. and O. Eriksson. 1997. Local colonization and extinction of field layer plants in a deciduous forest and their dependence on life history features. *Journal of Vegetation Science* 8:395–400.
- Gaston, K.J. 1994. *Rarity*. New York, NY: Chapman & Hall.
- Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57:845–858.
- Goodwillie, C. and C.L. Jolls. 2014. Mating systems and floral biology of the herb layer: A survey of two communities and the state of our knowledge. Pages 109–130 in F.S. Gilliam (ed.), *The Forest Herbaceous Layer in Forests of Eastern North America*, second edition. Oxford, UK: Oxford University Press.
- Graae, B.J., T. Hansen and P.B. Sunde. 2004. The importance of recruitment limitation in forest plant species colonization: a seed sowing experiment. *Flora* 199:263–270.
- Gutterman, Y. 2000. Maternal effects on seeds during development. Pages 59–84 in M. Fenner (ed.), *Seeds: The Ecology of Regeneration in Plant Communities*, second edition. Oxford, UK: Oxford University Press.
- Harmes, T.M. and C.M. Mabry. *In prep.* Modeling survival, productivity and persistence in forest perennial herbaceous species.
- Jacobsson, A. and O. Eriksson. 2002. Seed size and frequency patterns of understory plants in Swedish deciduous forests. *Eco-Science* 9:74–78.
- Jolls, C.L. and D. Whigham. 2014. Populations of and threats to rare plants of the herb layer: Still more challenges and opportunities for conservation biologists. Pages 134–163 in F.S. Gilliam (ed.), *The Forest Herbaceous Layer in Forests of Eastern North America*, second edition. Oxford, UK: Oxford University Press.
- Jules, E. 1998. Habitat fragmentation and demographic change for a common plant: *Trillium* in old growth forest. *Ecology* 79:1645–1656.
- Lenhard, W. and A. Lenhard. 2016. Computation of effect sizes. www.psychometrica.de/effect_size.html. *Psychometrica* <https://doi.org/10.13140/RG.2.2.17823.92329>.
- Leishman, M.R. and M. Westoby. 1994. The role of large seed size in shaded conditions: Experimental evidence. *Functional Ecology* 8:205–214.
- Mabry, C.M. 2000. Floristic analysis of central Iowa woodlands, and comparison of reproduction and regeneration in common and restricted herbaceous species. PhD Dissertation, Iowa State University.
- Mabry, C.M. 2002. Effects of cattle grazing on woodlands in central Iowa. *Journal of the Iowa Academy of Science* 109:53–60.
- Mabry, C.M. 2004. The number and size of seeds in common versus restricted woodland herbaceous species in central Iowa, USA. *Oikos* 107:497–504.
- Mabry, C.M. and J. Fraterrigo. 2009. Species traits as generalized predictors to forest community response to human disturbance. *Forest Ecology and Management* 257:723–730.
- Menges, E.S. 2008. Restoration demography and genetics of plants: When is a translocation successful? *Australian Journal of Botany* 56:187–196.
- Mottl, L.M., C.M. Mabry and D.R. Farrar. 2006. Seven-year survival of perennial herbaceous transplants in temperate woodland restoration. *Restoration Ecology* 14:330–338.
- Murray, B.R., P.H. Thrall, A.M. Gill and A.B. Nicotra. 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecology* 27: 291–310.
- Nuzzo, R. 2014. Statistical errors. *Nature* 506:150–152.
- Petersen, P.M. and M. Philip. 2001. Implantation of forest plants in a wood on former arable land: A ten year experiment. *Flora* 196:286–291.
- Reader, R.J. 1993. Control of seedling emergence by ground cover and seed predation in relation to seed size for some old field species. *Journal of Ecology* 81:169–175.
- Roberts, M.R. and F.S. Gilliam. 2014. Response of the herbaceous layer to disturbance in eastern forests. Pages 321–339 in F.S. Gilliam (ed.), *The Forest Herbaceous Layer in Forests of Eastern North America*, second edition. Oxford, UK: Oxford University Press.
- Rust, R.W. and R.R. Roth. 1981. Seed production and seedling establishment in the mayapple, *Podophyllum peltatum* L. *The American Midland Naturalist* 105:51–60.
- Silvertown, J. and M. Dodd. 1997. Comparing plants and connecting traits. Pages 3–16 in Silvertown J., M. Franco and J.L. Harper (eds.), *Plant Life Histories: Ecology, Phylogeny and Evolution*. Cambridge, UK: Cambridge University Press.
- Sobey, D.G. and P. Barkhouse. 1977. The structure and rate of growth of the rhizomes of some forest herbs and dwarf shrubs of the New Brunswick—Nova Scotia border region. *The Canadian Field-Naturalist* 91:377–383.
- Sultan, S.E. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evolutionary Biology* 21:127–178.
- Turnbull, L.A., M.J. Crawly and M. Rees. 2000. Are plant populations seed-limited: A review of seed sowing experiments. *Oikos* 88:225–238.
- van der Linden, P.J. and D.R. Farrar. 2011. *The Forest and Shade Trees of Iowa*, third edition, Iowa City, IA: University of Iowa Press.
- Vellend, M. 2005. Land-use history and plant performance in populations of *Trillium grandiflorum*. *Biological Conservation* 124: 217–224.
- Verheyen, K., G.R. Gutenspergen, B. Biesbrouck and M. Hermy. 2003. An integrated analysis of the effects of past land use on forest herb colonization at a landscape scale. *Journal of Ecology* 91:731–742.
- Whigham, D.F. 2004. Ecology of woodland herbs in temperate deciduous forests. *Annual Review of Ecology, Evolution and Systematics* 35:583–621.

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