

Research Article

Cite this article: Nebhut AN and Dukes JS (2023) Invasion by Callery pear (*Pyrus calleryana*) does not affect understory abundance or diversity in early-successional meadows. *Invasive Plant Sci. Manag* **16**: 215–224. doi: [10.1017/inp.2023.28](https://doi.org/10.1017/inp.2023.28)

Received: 16 May 2023
Revised: 18 August 2023
Accepted: 20 October 2023
First published online: 6 November 2023

Associate Editor:
Jacob N. Barney, Virginia Tech

Keywords:
Biological invasion; forest regeneration;
invader impact; succession

Corresponding author:
Andrea N. Nebhut;
Email: anebhut@stanford.edu

Invasion by Callery pear (*Pyrus calleryana*) does not affect understory abundance or diversity in early-successional meadows

Andrea N. Nebhut¹  and Jeffrey S. Dukes² 

¹Graduate Student, Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA; current: Graduate Student, Department of Biology, Stanford University, Stanford, CA, USA and ²Professor, Department of Forestry and Natural Resources and Department of Biological Sciences, Purdue University, West Lafayette, IN, USA; current: Senior Staff Scientist, Department of Global Ecology, Carnegie Institution for Science, Stanford, CA, USA; and Professor (by courtesy), Departments of Biology and Earth System Science, Stanford University, Stanford, CA, USA

Abstract

Trait differences between invasive plants and the plants in their recipient communities moderate the impact of invaders on community composition. Callery pear (*Pyrus calleryana* Decne.) is a fast-growing, stress-tolerant tree native to China that has been widely planted for its ornamental value. In recent decades, *P. calleryana* has naturalized throughout the eastern United States, where it spreads rapidly and achieves high abundance in early-successional environments. Here we compare the impacts of low-density, establishment-phase *P. calleryana* to those of functionally similar native trees on the understory community diversity and total cover of three early-successional meadows in Indiana's Eastern Corn Belt Plains. In contrast to our prediction that *P. calleryana* would have greater negative effects on the total abundance and diversity of the understory plant community compared with native tuliptree (*Liriodendron tulipifera* L.), American sycamore (*Platanus occidentalis* L.), or non-tree control plots, we found that these low-density populations of *P. calleryana* had no significant impact on total cover, species richness, or diversity indices for the understory community compared with the native trees and non-tree control plots. Likewise, the studied populations of *P. calleryana* had no significant impact on the native, introduced, woody, or native tree subsets of the understory community. These results indicate that in young, low-density populations situated in early-successional meadows, the trait differences between *P. calleryana* and functionally similar native trees are not of a great enough magnitude to produce changes in community composition. Going forward, complementary research on the impacts of *P. calleryana* on community composition and ecosystem processes in areas with long-established, dense invasions or invasions in more sensitive ecosystems would allow us to more fully understand how this widespread invader disrupts its host ecosystems.

Introduction

Ecological communities arise from complex interactions of biotic and abiotic factors across spatial and temporal scales (Díaz et al. 2007; Garnier et al. 2004; Heemsbergen et al. 2004; Zirbel et al. 2017). All organisms in an environment shape the community, but particular species may have outsized effects on their communities by mediating the fluxes of energy and materials within ecosystems or by altering the rates of these processes by transforming regulatory abiotic conditions (Chapin et al. 2000). Many attributes of an invader and its environment may contribute to both the capacity of an invader to spread and reach high abundances and to its impact once it has successfully established, but invasive species are generally expected to displace species to which they are functionally similar but competitively superior (MacDougall et al. 2009). Therefore, to understand the impact of common invaders on their communities, it is useful to understand how invaders alter their recipient communities relative to functionally similar native species.

Callery pear (*Pyrus calleryana* Decne.) is a widespread invader throughout the eastern United States. Originally introduced from China in 1908 as a fire blight-resistant rootstock for the edible French pear (*Pyrus communis* L.), one cultivar of the tree, known as the Bradford pear, became a popular ornamental in the 1960s due to its showy flowers, disease resistance, and environmental tolerance (Culley 2017; Niemiera 2018). While the ornamental cultivars were initially believed to be sterile, the tree first escaped cultivation in 1964, and naturalized individuals became commonplace in the 1980s (Culley 2017). The tree's rate of spread accelerated over time, and *P. calleryana* is now widespread in the eastern United States (Vincent 2005); 4% of Indiana family forest owners (Clarke et al. 2019) and 8% of Illinois landowners (Clarke et al. 2017) report occurrences of naturalized *P. calleryana* on their properties. Growing

© The Author(s), 2023. Published by Cambridge University Press on behalf of Weed Science Society of America. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.



Management Implications

Pyrus calleryana (Callery pear) is a popular ornamental tree across the eastern United States, with large populations of naturalized *P. calleryana* throughout its introduced range. The tree's long-lived seeds, thorny phenotype, and resprouting capacity make controlling established populations cost- and labor-intensive. Managers actively remove *P. calleryana* throughout the region, but few studies have characterized the impacts of this species on its recipient communities and ecosystems. We examined these impacts by comparing understory communities surrounding invasive *P. calleryana* individuals with those around two functionally similar native tree species, tulip tree (*Liriodendron tulipifera* L.) and American sycamore (*Platanus occidentalis* L.), in early-successional meadow environments in Indiana's Eastern Corn Belt Plains with low-density, establishing populations of *P. calleryana*. We found that at these low densities, the effect of *P. calleryana* did not differ significantly from the effects of native tree species for either the understory community as a whole or the native, introduced, woody, and native tree subsets of the understory community. As *P. calleryana* does not appear to alter the successional trajectories of meadow environments in the establishment-phase, low-density invasions investigated in this study, these results suggest that the removal of trees at this early stage could minimize the tree's long-term impacts on its recipient communities. Ideally, *P. calleryana* should be removed before flowering to prevent the introduction of abundant, long-lived seeds to the community, and potential seed sources should be removed from surrounding areas before novel populations are able to establish or reach high abundance.

public awareness and policy actions to limit new plantings and remove existing trees hold promise in limiting this tree's spread, but may be stymied by the introduction of new cultivars and the role of climate change in expanding the tree's potential range and landscape presence (Culley 2017). Given that this fast-growing tree has already reached high abundances in some areas and may be expected to continue increasing in density and range, understanding the effects of this tree on its environment and prioritizing the removal of the most damaging *P. calleryana* stands is a necessary component of an effective management strategy for this invasive tree.

Many attributes have been linked to the success of *P. calleryana* in escaping cultivation and spreading to natural environments, including aspects of the tree's environmental niche, physiology, and genetics. While *P. calleryana* has a wide environmental tolerance (Culley and Hardiman 2007), it frequently grows as an early-successional species in dry and high-light environments (Dunn 2018), where it may overshadow and outcompete shade-intolerant species in the sapling and regeneration layers. Additionally, *P. calleryana* may benefit from enemy release, as insect herbivores feed less on *P. calleryana* than on native trees in both no-choice assays and in the field (Hartshorn et al. 2022). Genetically, *P. calleryana* exhibits gametophytic self-incompatibility, which promotes outcrossing among genetically distinct cultivars (Culley and Hardiman 2009). Hybridization has been proposed as a mechanism for the evolution of invasiveness in plants, and recent evidence suggests that intra-taxon hybridization, like inter-taxon hybridization, may promote invasiveness by decreasing genetic load and increasing evolutionary novelty, genetic variation, and fixed heterosis (Gaskin 2017; Schierenbeck

and Ellstrand 2008). The prevalence of *P. calleryana* throughout the eastern United States is associated with the introduction of new cultivars and the practice of grafting, which together provide the trees with sufficient genetic variation to overcome self-incompatibility and form self-sustaining populations, alongside occasional hybridization with other *Pyrus* species (Connolly and Boutiette 2020; Culley et al. 2011; Hardiman and Culley 2010; Vincent 2005). Indeed, *P. calleryana* across the United States is characterized by high genetic diversity, high gene flow, and a structured population (Nowicki et al. 2022; Sapkota et al. 2021).

Pyrus calleryana also exhibits many traits associated with both stress tolerance and fast growth. The tree exhibits relatively long leaf phenology compared with native species and is resistant to short-term frost events, potentially allowing it to outcompete native species via its extended growing season (Maloney et al. 2022). Additionally, while the photosynthetic characteristics of *P. calleryana* are comparable to those of other woody deciduous species and measurements conducted by Merritt et al. (2014) indicate that it has a lower mean photosynthetic rate than those reported for woody invaders butterfly bush (*Buddleja davidii* Franch.) (Shi et al. 2006) and Norway maple (*Acer platanoides* L.) (Morrison and Mauck 2007), *P. calleryana* can adapt to its environment such that advanced-generation hybrids exhibit higher photosynthetic and transpiration rates than early-generation hybrids (Merritt et al. 2014). Once established in an environment, the tree's long-lived seeds, occasional thorny phenotype, fire resistance, and capacity to resprout after top-killing make controlling established populations cost- and labor-intensive (Coyle et al. 2021; Culley and Hardiman 2007; Hay 2021; Serota and Culley 2019; Warrix and Marshall 2018). Further, as genetic admixture between populations continues into advanced generations, the "cultivation-adapted" trees may lose detrimental traits associated with artificial selection and become more invasive (Hardiman and Culley 2010).

Despite a wealth of information on the environmental, physiological, and genetic drivers of *P. calleryana* naturalization success, there remains a dearth of studies about the effects of this introduced tree on its invaded communities and how these impacts compare with those of functionally similar native trees. One recent study suggests that *P. calleryana* allelopathically reduces the germination rate of common native grassland species (Woods et al. 2023). Additionally, several researchers have speculated from reports of functionally similar invaders that *P. calleryana* may alter nutrient cycling and successional trends (Culley and Hardiman 2007; Dunn 2018). The potential effects of *P. calleryana* on nutrient cycling are supported by Woods and colleagues' (2021) finding that *P. calleryana* invasion alters soil enzyme activities associated with carbon and nitrogen cycling, while the impact of *P. calleryana* on its recipient community, and thus succession, remains to be explored.

Here we investigate the impact of *P. calleryana* on succession through direct observations of the effect of establishment-phase *P. calleryana* on the understory community in the early-successional environments where it is most common as an invader. Left undisturbed, these early-successional meadows would be expected to follow a typical pattern of secondary succession involving further colonization and eventual dominance of woody species as they mature into the oak (*Quercus* spp.)–hickory (*Carya* spp.) forests that historically characterized the region (Bazzaz 1968; Drury and Nisbet 1973; Hobbs 2012; Oosting 1942). However, invasion can alter the successional trajectory of forests through alterations to nutrient cycling and the inhibition of tree

regeneration and growth (Flory and Clay 2010; Hartman and McCarthy 2007, 2008). Woodland succession is of particular concern in the American Midwest, where climate change, invasive species, and altered disturbance regimes have produced forests with a homogenized structure, reduced productivity, and low resistance and resilience to stressors (Alexander et al. 2021; Dey et al. 2019). Invasive emerald ash borers (*Agrilus planipennis*) have decimated ash (*Fraxinus* spp.) populations throughout the area (Herms and McCullough 2014), and *Quercus* declines are well documented in the region (Abrams 2003; Dey 2014), with invasive plant species being implicated as a contributing factor (Hartman and McCarthy 2004; Ward et al. 2018). The role of plant invaders in *Quercus* declines may be especially prominent in high-light, high-nutrient sites and along forest edges, where *P. calleryana* is a frequent invader (Dunn 2018; Schulte et al. 2011).

In particular, *P. calleryana* may be expected to disrupt its understory environment, because fast-growing, resource-acquisitive plants such as *P. calleryana* frequently display traits such as dense canopies, high transpiration rates, and low litter C:N values (Reich 2014) that alter the microclimate and soil chemistry of their surrounding area (Ehrenfeld 2003; Ehrenfeld et al. 2001; Jo et al. 2017; Liao et al. 2008; Skurski et al. 2014; Weidenhamer and Callaway 2010). These alterations may enable *P. calleryana* to stabilize or accelerate its own and other invasions by enhancing the growth of invaders relative to natives and providing habitats for new invasion (Siemann and Rogers 2003). The potential effects of *P. calleryana* invasion may be blunted, however, in the disturbed, early-successional meadow environments where *P. calleryana* is a frequent invader, because these systems are typically already heavily invaded and high in nutrients. In these systems, *P. calleryana* may act a “back-seat driver” of community change, both benefiting from disruptions that favored its establishment and led to initial declines in native species and contributing to further changes in ecosystem processes that further reduce native diversity and benefit its growth (Bauer 2012). Therefore, while *P. calleryana* may produce multiplicative effects on native diversity and abundance in concert with the sites’ disturbance histories and other ongoing invasions, these effects may not be as severe as if *P. calleryana* entered relatively “pristine” environments with higher initial diversity and more disturbance-sensitive species. The low densities of establishment-phase populations may additionally curtail the potential effects of *P. calleryana*, as invader impacts are often highly dependent on their abundance (Sofaer et al. 2018).

In this study, we investigate how establishment-phase *P. calleryana* alters the abundance and diversity of Indiana’s early-successional meadow environments during its establishment phase. We predicted that invasive *P. calleryana* trees would reduce overall abundance and diversity, producing communities with relatively low diversity and cover of native species but higher abundance and diversity of nonnatives. We expected that *P. calleryana* would most strongly influence the woody subset of the understory community, particularly the native trees.

Materials and Methods

Study Sites

We investigated the effects of *P. calleryana* invasion on early-successional understory communities at three field sites in central Indiana, USA: Burnett Woods Nature Preserve (BWNP; 39.750°N, 86.367°W), a privately owned property in Crawfordsville (CRAW; 39.992°N, 86.917°W), and Sargent Road Nature Park (SRNP;

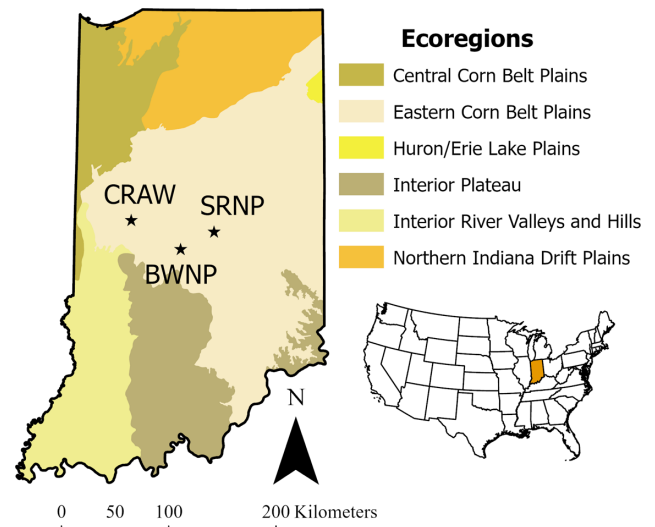


Figure 1. Field site locations and major ecoregions of Indiana (US Environmental Protection Agency 2011) and location of Indiana within the United States. Site abbreviations include Burnett Woods Nature Preserve (BWNP), Crawfordsville property (CRAW), and Sargent Road Nature Park (SRNP).

39.902°N, –86.012°W). All three sites host low-density, establishment-phase populations of *P. calleryana*, with densities ranging from single to dozens of individuals per hectare. These populations may be considered a lower bound of the species’ abundances in invaded habitats regionally, with high-density populations reaching tens of thousands of stems per hectare (Boyce and Ocasio 2020; Dunn 2018; Warrix and Marshall 2018).

Each of these field sites lies within the loamy, high lime-till plains of Indiana’s eastern Corn Belt plains (Figure 1), a region historically characterized by hardwood forests and currently dominated by extensive corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] production. The ecoregion is temperate, with a humid continental climate defined by hot summers (16 to 18 C [min.] to 30 to 32 C [max.] in July), cold winters (–7 to –4 C [min.] to 3 to 6 C [max.] in January), and 864 to 1,143 mm of annual precipitation (Wiken et al. 2011).

BWNP is a publicly accessible park owned by the Central Indiana Land Trust and surrounded by residential neighborhoods. The 32-ha property has Crosby and Miami silt loam soils and is dominated by mature woodlands, with a 3-ha plot of early-successional meadow in its center, which was utilized in this study. The early-successional meadow had previously been under agricultural production before being acquired by the land trust in 2010, at which point it was planted with a mix of *Quercus* and *Carya* to match the composition of the surrounding woods and has since been periodically treated for invaders, including *P. calleryana* and honeysuckle (*Lonicera* spp.). CRAW is a 6-ha, privately held property with St. Charles silt loam soil surrounded by agricultural land in soybean and corn cultivation. The property is primarily wooded but includes a 2-ha meadow that was in agricultural production until 2009, at which point it was left fallow and mowed annually through 2013, after which it was allowed to grow naturally, with the exception of mowed paths throughout the meadow and occasional removal of poison ivy (*Toxicodendron radicans* L.). Finally, SRNP is a park owned by the Mud Creek Conservancy and surrounded by residential neighborhoods, with Ockley and Sloan silt loam soils (Soil Survey Staff 2023). The 10-ha property includes mature forest, wetlands, and 4 ha of

early-successional meadows utilized in this study. This site was in agricultural production through approximately 1995, at which point it lay fallow, and has experienced some targeted *Lonicera* removal beginning in 2019.

Vegetation Surveys

We conducted vegetation surveys of each field site between July 6 and July 29, 2021. At each field site, we surveyed areas around 10 haphazardly selected trees of each of three species: *P. calleryana*, tuliptree (*Liriodendron tulipifera* L.), and American sycamore (*Platanus occidentalis* L.). We selected these as our comparison species because they were abundant at each site and are commonly noted as early-successional species in old fields in the American Midwest (Wells and Schmidting 1990). All surveyed trees were small and presumably young, ranging from 1.1 to 18.9 cm in diameter at breast height (DBH mean: 6.9 ± 4.5 cm; Supplementary Figure S2). We also surveyed 10 control plots with no overtopping trees at each site. This generated a total of 40 sampling plots per site and 120 plots across all sites. At each of these plots, we conducted a visual estimate of the percent canopy cover of all understory vascular plant species within a 1-m² square frame as our proxy for the abundance of each species in each plot. We defined canopy cover as the percentage of the area in the square frame covered by a projection of the outermost perimeter of the plant, meaning that overlapping plants could result in a greater than 100% cover estimate for a given plot. For sampling plots with a focal *P. calleryana*, *P. occidentalis*, or *L. tulipifera* tree, the focal tree stem was centered in the middle of the plot and was not included in the percent cover measurement. However, when other individuals of these same species were in the study plot understory, we included them in the vegetation surveys. We selected 1 m² as our sampling plot size, centered on the tree, to capture the effects immediately under the tree where the leaves fall and the roots are likely to be the densest, and to avoid any diminishing effects farther from the canopy that might have been produced by a larger sampling quadrant (Amiotti 2000; Pallant and Riha 1990). As the basal diameter of the trees themselves covered a mean of only 0.39% of the plot area ($\pm 0.05\%$ SE; range: 0.01–2.81%), the trunks of the trees themselves had minimal impact on the estimate of total understory cover. All raw data sets can be found Supplementary Material 1 and 2.

Data Analysis

All statistical analyses were conducted in R (v. 1.3.1073; R Core Team 2020) and the complete R script can be found in Supplementary Material 3. We evaluated the understory plant community based on species richness (*S*), total cover, Shannon's index (*H*), and Simpson's index (*D*). Species richness was defined as the number of vascular plant species in the plot. We calculated total cover as the sum of all species-specific cover values in a plot. Finally, we utilized R package VEGAN (Oksanen et al. 2020) to calculate the Shannon's and Simpson's diversity indices.

To test the relationship between each of the diversity indices and plot type (*P. calleryana*, *P. occidentalis*, *L. tulipifera*, or control), we fit a series of linear models with each community index as the outcome variable and the field site, plot type, and the interaction between field site and plot type as the predictor variables ($n = 120$). Field site was included as a fixed effect, rather than a random effect, due to the difficulty of accurately estimating group-level variation in random effects with fewer than five levels (Harrison 2015). In addition, we tested the potential effect of tree

size on each of the community indices by fitting a series of linear models with each community index as the outcome variable and the field site, tree species, tree DBH, and their interactions as the outcome variables. We included these interactions in the model because the sensitivity of the community indices to tree species and size may vary with site; that is, if some sites are more diverse overall and contain more disturbance-sensitive species, they may be more sensitive to the changing environmental conditions associated with older and larger trees, resulting in greater decreases in diversity than low-diversity sites without disturbance-sensitive species. As the non-tree control plots did not have a DBH, we excluded all control plots from this set of tests ($n = 90$). Finally, we additionally conducted these analyses with separate per-site models to better understand how the effects of *P. calleryana* may vary between locations; this analysis can be found in Supplementary Material 4 (Supplementary Figures S6–S9; Supplementary Tables S5 and S6).

We assessed whether these models met the homogeneity of variances and normality of residuals assumptions by visually checking the residual normal probability plot and the normal Q-Q plot. All model assumptions were satisfied, so we proceeded without transformations. When the overall linear model was statistically significant ($\alpha = 0.05$), we tested the significance of the relationships between output and predictor variables with an ANOVA followed by post hoc Tukey's honest significant difference tests utilizing R package STATS (R Core Team 2020), then quantified effect size with the ω^2 value calculated by R package SJSTATS (Lüdtke 2021). We conducted this analysis for the entire understory vascular plant community and then repeated it for the native understory plant community, the introduced understory plant community, the understory woody community, and the understory native tree community. By analyzing both the whole community and these community subsets, we are able to better understand how *P. calleryana* altered community composition in addition to overall diversity and abundance. For instance, investigating the native and invasive subsets of the community separately allowed us to detect changes that might have been missed otherwise if, for instance, losses in native plant species driven by *P. calleryana* were paired with concurrent gains in invasive plant species such that there would be no difference in overall community diversity. Additionally, this method allowed us to test the relative sensitivity of these community subsets to *P. calleryana* invasion, which was necessary to test our prediction that *P. calleryana* would have the strongest negative effects on native woody trees.

Results and Discussion

Understory community characteristics varied substantially across the three field sites (Figure 2; Supplemental Figure S1; Supplemental Table S2). Across all sites, a total of 125 species were detected, with the most dominant being common species of low conservation value, such as Canada goldenrod (*Solidago canadensis* L.) and *T. radicans*. BWNP was the most diverse site, with a total of 69 detected understory species ($H = 3.03$; $D = 0.90$), followed by SRNP, with 73 detected understory species ($H = 2.76$; $D = 0.89$), and finally CRAW, with 53 detected understory species ($H = 1.87$; $D = 0.67$). All sites were heavily invaded by understory invaders common in the region, such as rambler rose (*Rosa multiflora* Thunb.) and meadow fescue [*Schedonorus pratensis* (Huds.) P. Beauv.] (Supplemental Table S1). This species composition and relative lack of diversity is typical of early-successional old field ecosystems in the region (Hopkins and Wilson

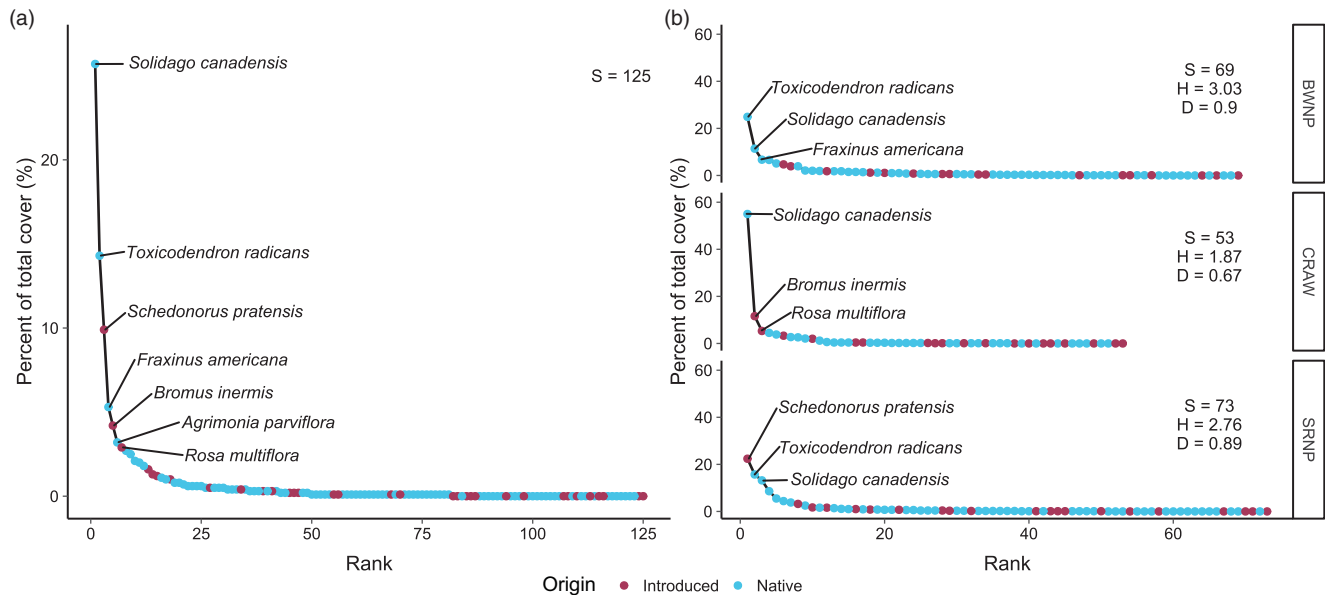


Figure 2. Species rank-abundance curves (A) across all field sites and (B) separated by field site. Shown are species by rank and proportion of total cover (%), and species richness (S), Shannon’s index (H), and Simpson’s index (D). Site abbreviations as in Figure 1.

1974; Root and Wilson 1974), whose global economic ties, disturbance history, and low relative biodiversity make them highly susceptible to invasion (Gross and Emery 2007; Wiedenmann 2001).

We anticipated that plots containing *P. calleryana* would be less diverse and less abundant than either the control plots or plots containing other tree species because of the potential effects of *P. calleryana* on microclimate and nutrient cycling; however, our results do not support this hypothesis. Across the entire understory community, patterns of species richness and total cover were affected only by field site, with only Shannon’s and Simpson’s indices of diversity changing with both field site and plot type (Tables 1 and 2). Pairwise comparison of Shannon’s and Simpson’s diversity indices between plot types indicates that understory community diversity did not differ between *P. calleryana* and any other plot types; instead, the only significant pairwise comparison for both Shannon’s and Simpson’s diversity indices was between *L. tulipifera* and the control plots, with *L. tulipifera* plots having 15.2% higher Shannon’s diversity and 12.9% higher Simpson’s diversity than the control plots (Figures 3 and 4).

These results suggest that at this early, low-density establishment phase, *P. calleryana* has little, if any, impact on the abundance or species diversity of the early-successional understory communities investigated in this study. These metrics do not account for species composition, however. Given the highly invaded nature of these early-successional understory environments and the propensity for invasive species to promote the success of other invasive species through alterations to their shared environment, it is possible that *P. calleryana* might offset its potential negative effect on the native understory community through concurrent positive effects on the introduced understory community. We tested this prediction by subsetting our data into just the native and introduced portions of the understory community and fitting our linear models of community indices to each. For many of these subsets, the resulting statistical models explained little of the observed variability in species richness, total cover, or Shannon’s or Simpson’s indices of diversity. We did not find our anticipated pattern of increasing introduced species

diversity and cover paired with a concurrent decrease of native species diversity and cover in *P. calleryana*-invaded plots (Tables 1 and 2). Instead, our models of plot type and site either failed to explain any of the observed variation in the community indices or found only a significant effect of site (Table 1). Therefore, in addition to having no significant effect on the overall total cover or diversity of the understory community as a whole, *P. calleryana* had no detectable effect on the total cover or diversity of native and invasive plants within the understory community.

To investigate the impacts of *P. calleryana* on the woody understory community, we subsetted the understory community into both woody species as a whole and native tree species and found no effect of *P. calleryana*. Woody total cover varied with site and plot type (Tables 1 and 2), but a pairwise comparison of total woody cover between plot types indicated that there was no difference in total woody cover between *P. calleryana* and any of the other plot types; instead, only *P. occidentalis* plots had 156.1% higher woody cover than the control plots (Figure 5). Otherwise, the woody understory community reflected the trend of the overall understory community in that plot-level variation in woody species richness and woody Shannon’s index was driven by site, not plot type (Tables 1 and 2). When we partitioned the woody understory community into just the native tree community, we found that the observed variation in the community indices was likewise explained by site alone (Table 2).

When accounting for differences in tree size, we likewise found no differences between the impacts of *P. calleryana* and the comparison species on community abundance or diversity for either the entire understory community or its native, invader, woody, or native tree subsets (Supplementary Table S3). Site alone explained the observed variability in diversity or total cover for all models except those of Shannon’s index of the native community and those of the total cover and Shannon’s index of the entire understory community (Supplementary Table S4; Supplementary Figures S3–S5). For each of these models, post hoc pairwise comparison among tree species revealed only differences in *L. tulipifera* and *P. occidentalis* for total cover (Supplementary Figure S3), but no significant differences

Table 1. Linear model results of the community indices by community subset.^a

Community	Species richness (<i>S</i>)			Total cover (%)			Shannon index (<i>H</i>)			Simpson index (<i>D</i>)		
	<i>F</i>	<i>P</i>	Adjusted <i>R</i> ²	<i>F</i>	<i>P</i>	Adjusted <i>R</i> ²	<i>F</i>	<i>P</i>	Adjusted <i>R</i> ²	<i>F</i>	<i>P</i>	Adjusted <i>R</i> ²
Entire understory community	5.594	<0.001	0.30	2.144	0.02	0.10	13.15	<0.001	0.53	11.17	<0.001	0.49
Native community	10.53	<0.001	0.47	0.97	0.47	<0.01	18.02	<0.001	0.61	19.91	<0.001	0.64
Introduced community	0.784	0.66	-0.02	2.114	0.03	0.09	1.374	0.20	0.03	1.513	0.14	0.04
Woody community	3.958	<0.001	0.21	4.741	<0.001	0.26	4.741	<0.001	0.26	0.952	0.49	<0.01
Native tree community	4.432	<0.001	0.24	4.442	<0.001	0.24	4.442	<0.001	0.24	4.34	<0.001	0.23

^aSignificant P-values shown in bold, and marginal P-values shown in italics.

Table 2. ANOVA results of the linear models of community diversity indices by tree species, site, and the interaction of site and species.^a

Community	Variable	Species richness (<i>S</i>)			Total cover (%)			Shannon index (<i>H</i>)			Simpson index (<i>D</i>)		
		<i>F</i>	<i>P</i>	ω^2	<i>F</i>	<i>P</i>	ω^2	<i>F</i>	<i>P</i>	ω^2	<i>F</i>	<i>P</i>	ω^2
Entire understory community	Plot type	0.976	0.41	<0.001	2.505	0.06	0.034	3.008	0.03	0.025	2.704	0.05	0.022
	Site	24.940	<0.001	0.281	6.073	<0.001	0.077	64.757	<0.001	0.503	54.252	<0.001	0.459
	Plot type × site	1.45	0.20	0.016	0.653	0.69	-0.016	0.995	0.43	0.000	1.037	0.41	0.001
Native community	Plot type	1.826	0.15	0.011				2.38	<i>0.07</i>	<i>0.013</i>	1.883	0.14	0.008
	Site	51.617	<0.001	0.450				92.509	<0.001	0.596	102.383	<0.001	0.618
	Plot type × site	1.189	0.32	0.005				1.003	0.43	0.000	1.426	0.21	0.008
Introduced community	Plot type				1.148	0.33	0.003						
	Site				7.604	<0.001	0.100						
	Plot type × site				0.766	0.60	-0.011						
Woody community	Plot type	1.171	0.32	0.003	4.997	<0.001	0.074	0.300	0.83	-0.014			
	Site	19.060	<0.001	0.237	15.562	<0.001	0.181	20.556	<0.001	0.257			
	Plot type × site	0.3179	0.93	-0.027	1.017	0.42	0.001	0.213	0.97	-0.031			
Native tree community	Plot type	0.906	0.44	-0.002	2.014	0.12	0.019	1.382	0.25	-0.008	0.287	0.84	-0.014
	Site	20.613	<0.001	0.249	20.001	<0.001	0.241	10.737	<0.001	0.141	18.329	<0.001	0.221
	Plot type × site	0.801	0.57	-0.008	0.469	0.83	-0.020	0.596	0.73	-0.018	1.704	0.13	0.027

^aAreas with an insignificant statistical model (see Table 1) are omitted. Significant P-values shown in bold, and marginal P-values shown in italics.

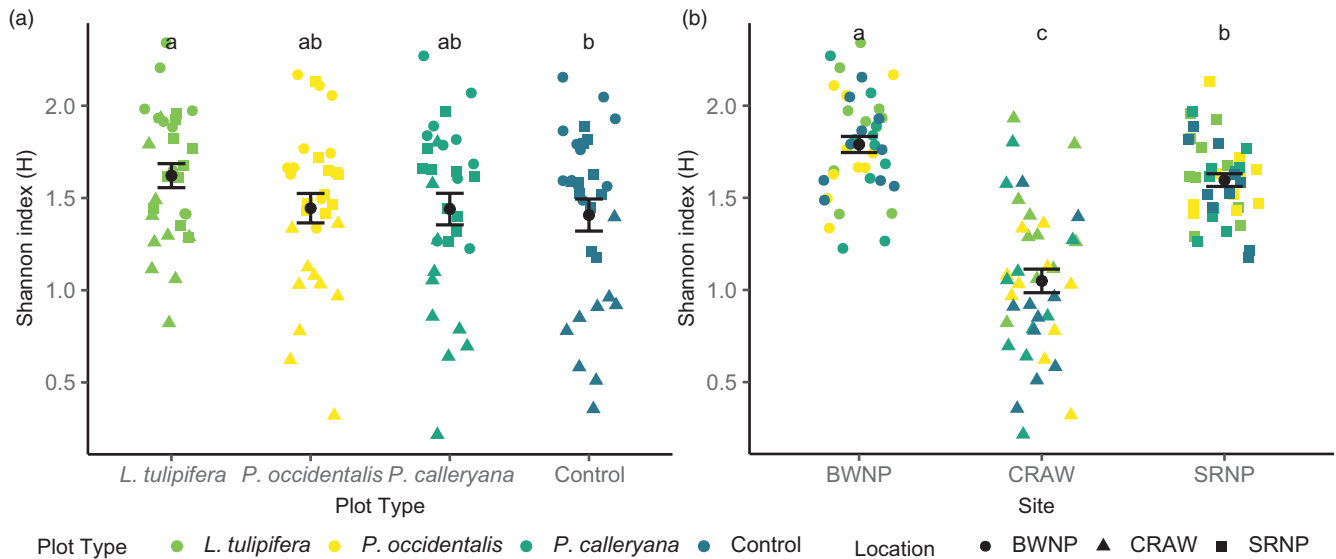


Figure 3. Plot-level Shannon index (H ; $n = 120$) by (A) plot type and (B) site. Shown are data points and mean \pm SE; average values with the same letter code within each panel are not significantly different from each other. Site abbreviations as in Figure 1.

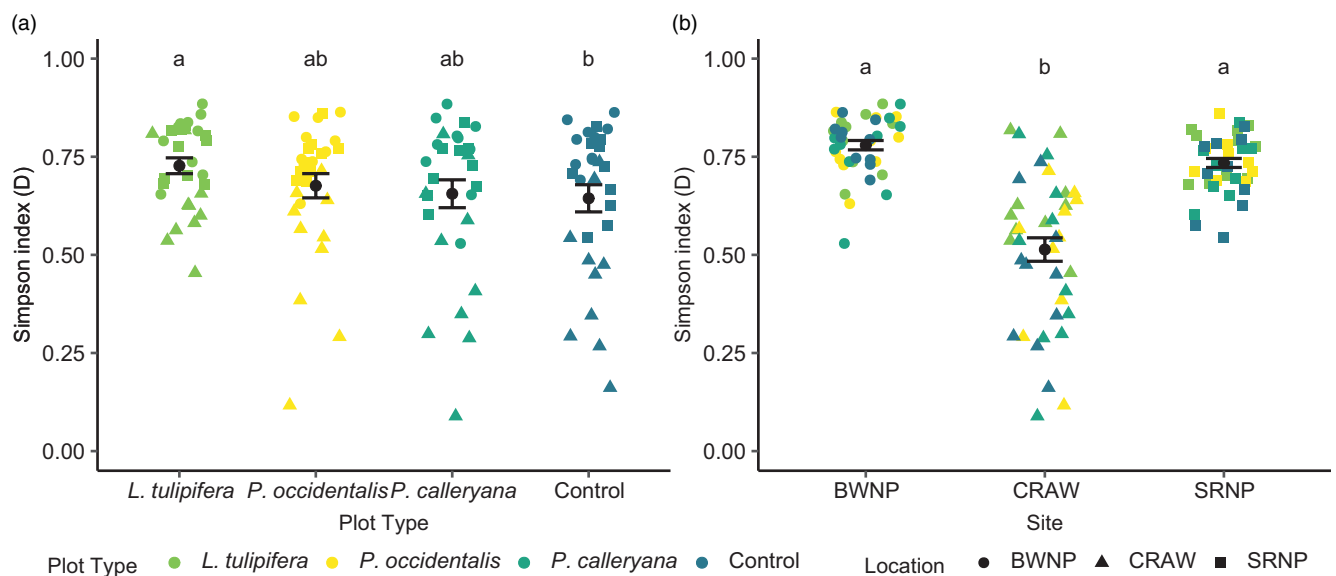


Figure 4. Plot-level Simpson's index (D ; $n = 120$) by (A) plot type and (B) site. Shown are data points and mean \pm SE; average values with the same letter code within each panel are not significantly different from each other. Site abbreviations as in Figure 1.

among tree species for the total community Shannon's diversity (Supplementary Figure S4) or native community Shannon's diversity (Supplementary Figure S5). We found no effect of tree size on any of the community indices, either as a main effect or with tree species or site.

As a whole, these results indicate that at the low densities investigated in this study, *P. calleryana* did not produce a detectable shift in understory diversity or abundance, either for the entire understory community or for the native, introduced, woody, or native tree subsets of the community. This result may be explained by an insufficient trait difference between *P. calleryana* and the native trees to produce changes in the understory community at these early-successional meadow sites, where baseline diversity is low and *P. calleryana* invasion was relatively new and the trees were relatively sparse.

Whereas invasive plants frequently have traits that promote changes in nutrient cycling and microclimate, these traits vary considerably among invasive species and must generally fall outside the range of common resident species for an invader to have large per capita effects on its recipient system. Current reports on *P. calleryana* physiology and community or ecosystem impacts suggest that these trees may not exhibit many of the common leaf traits associated with both invasiveness—and thus high abundance—and high per capita effects. That is, while *P. calleryana* might be expected to have high rates of leaf gas exchange compared with native trees, given their status as fast-growing invaders, Merritt et al. (2014) found that the trees exhibit moderate leaf gas exchange values that fall well within the range of photosynthetic rates reported by other studies of comparable deciduous woody species. These moderate gas exchange values suggest that photosynthetic

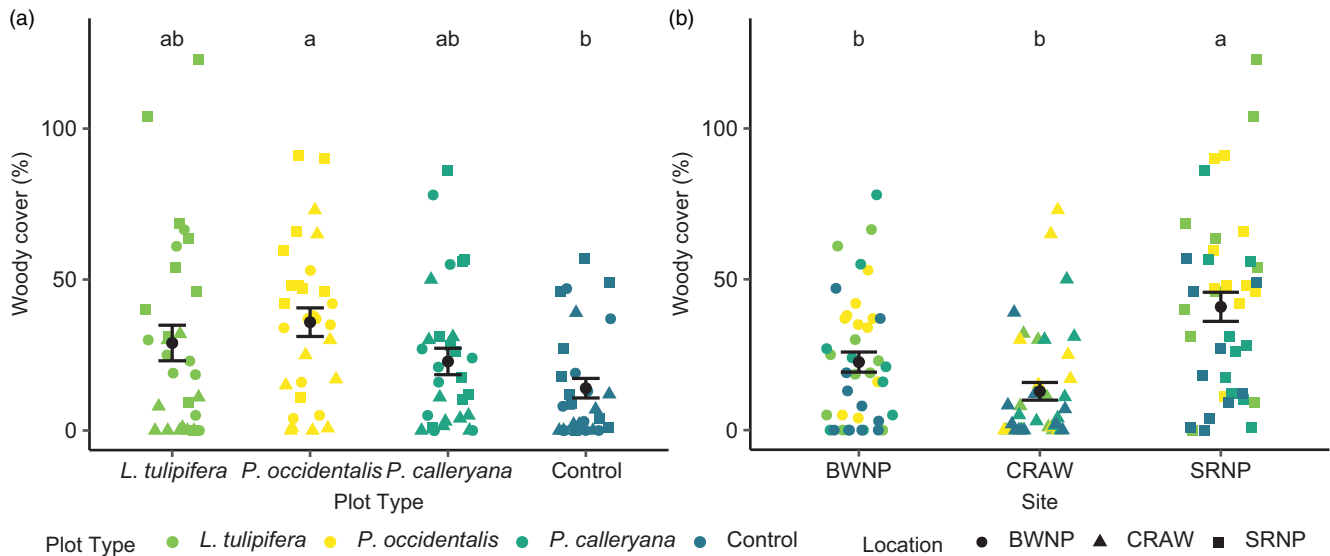


Figure 5. Plot-level woody cover (%; $n = 120$) by (A) plot type and (B) site. Shown are data points and mean \pm SE; average values with the same letter code within each panel are not significantly different from each other. Site abbreviations as in Figure 1.

characteristics may not be a major source of invasiveness in this species, and therefore predictions for ecosystem impacts resulting from a supposedly high photosynthetic rate may be dubious. Alterations in soil nitrogen dynamics may also not be dramatic. That is, while many fast-growing invasives like *P. calleryana* have low C:N and quickly decomposing litter, *P. calleryana* has a similar C:N ratio to *P. occidentalis*, a higher C:N ratio than the functionally similar invader Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder], and similar overall decomposition dynamics to red maple (*Acer rubrum* L.), an abundant native tree throughout its eastern North American range (Boyce 2022). As a result of these moderate trait values, which fall within the range of other common species in its recipient ecosystems, *P. calleryana* would be expected to have a low per capita effect on its surrounding community and ecosystem.

Instead, potential *P. calleryana* impacts may be driven by high abundance, as even small trait differences resulting in small per capita effects can result in detectable changes in community diversity at high invader densities. *Pyrus calleryana* may achieve these high densities via high seed production and germination rates (Serota and Culley 2019) and generalist pollination and dispersal methods (Culley and Hardiman 2009; Dunn 2018; Farkas et al. 2002), which, exacerbated by the widespread planting of these trees as ornamentals, results in substantial propagule pressure. Indeed, *P. calleryana* is capable of forming dense, monocultural thickets (Culley and Hardiman 2007) and likely has the largest impact on its surroundings when growing in these thickets. As the *P. calleryana* trees utilized in this study were in their establishment phase, with scattered individuals occurring at approximate densities of single to dozens of trees per hectare, the lack of impacts observed in this study may illustrate a lower bound for the species' influence across a density gradient. Greater impacts might be observed in established populations with high density, such as the hundreds to tens of thousands of stems per hectare reported by Dunn (2018), Warrix and Marshall (2018), and Boyce and Ocasio (2020).

As invader per capita effects compound over time, often on the scale of decades to centuries, time since invasion further alters overall invader impacts (Eviner et al. 2012; Strayer et al. 2006). For example, Sydney golden wattle [*Acacia longifolia* (Andrews)

Willd.] alters nitrification rates and litter accumulation within the first 10 yr of establishment but takes more than 20 yr to produce measurable impacts on nutrient sequestration (Marchante et al. 2008). The impacts of *P. calleryana* on soil organic matter and nitrogen availability would be expected to be of a smaller magnitude than those produced by *A. longifolia*, as *P. calleryana* is not a nitrogen fixer and has comparable C:N values to other common species in its recipient communities (Boyce 2022), and would therefore take longer to accrue large enough changes to alter the understory community. Given that the *P. calleryana* trees in this study were small (DBH mean: 6.9 ± 4.5 cm; Supplementary Figure S2) and therefore likely young and newly established, it is possible that the sites utilized in this study have not been invaded long enough to accumulate sufficiently large per capita changes in nitrogen cycling or other ecosystem functions to measurably alter the understory community. These changes may appear if the invasion is allowed to mature unabated.

Finally, the lack of *P. calleryana*-driven effects on understory abundance and diversity observed in this study may result from the relatively low baseline diversity of these highly invaded field sites, which is typical of early-successional meadow environments with a history of cultivation where past disturbances may have removed disturbance-sensitive species or those with long seedbank viability (Simberloff 2010; Souza et al. 2011). In these systems, the effects of disturbance, including increasing invasion, may follow an asymptotic relationship, with sharp decreases in native diversity observed at initial levels of disturbance and small decreases in native diversity occurring with later disturbances or with increasing invader abundances (Hart and Holmes 2013; Sax et al. 2007). Therefore, alongside high numbers and abundances of other invasive species, the multiplicative effects of relatively new and sparse *P. calleryana* invasions may be small, slow to accumulate, and difficult to detect.

These results should not be taken as an indication that *P. calleryana* has no potential effect on its host communities under other circumstances. Going forward, further research on the impacts of *P. calleryana* on ecosystem processes and community composition across density, time, and disturbance gradients, including the areas of high local density and long-established

invasions in otherwise “pristine” ecosystems, would allow us to better understand how this invader alters community composition. Understanding the mechanisms of invader impact and the relationship between density, time since invasion, disturbance history, and impact is crucial to determining the optimal management effort for an invasive species and preventing either over- or underinvestment in management (Levine et al. 2003; Yokomizo et al. 2009). Our findings indicate that in the young, sparse, establishment-phase invasions typical of Indiana’s early-successional meadow environments, the trait differences between *P. calleryana* and functionally similar native trees are not of a great enough magnitude to drive changes in community composition. Therefore, management to remove the invasive trees at this stage may forestall the disruptions to the environment’s successional trajectories that may potentially occur if the invasions are allowed to progress unimpeded to reach high densities and ages.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/inp.2023.28>

Acknowledgments. We thank the Central Indiana Land Trust for allowing us to conduct research at the Burnett Woods Nature Preserve, Mud Creek Conservancy for allowing us to conduct research at Sargent Road Nature Park, and Amy and Chad Westphal for allowing us to conduct research on their property. This research received no specific grant from any funding agency or the commercial or not-for-profit sectors. No conflicts of interest have been declared.

References

- Abrams MD (2003) Where has all the white oak gone? *BioScience* 53:927–939
- Alexander HD, Siegert C, Brewer JS, Kreye J, Lashley MA, McDaniel JK, Paulson AK, Renninger HJ, Varner MJ (2021) Mesophication of oak landscapes: evidence, knowledge gaps, and future research. *BioScience* 71:531–542
- Amiotti NM (2000) The impact of single trees on properties of loess-derived grassland soils in Argentina. *Ecology* 81:3283–3290
- Bauer JT (2012) Invasive species: “back-seat drivers” of ecosystem change? *Biol Invasions* 14:1295–1304
- Bazzaz FA (1968) Secondary Succession on Abandoned Fields in Southern Illinois. Ph.D thesis. Champaign: University of Illinois at Urbana-Champaign. 195 p
- Boyce RL (2022) Comparison of Callery pear (*Pyrus calleryana*, Rosaceae) leaf decomposition rates with those of the invasive shrub Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae) and two native trees, red maple (*Acer rubrum*, Sapindaceae) and American sycamore (*Platanus occidentalis*, Platanaceae). *J Torr Bot Soc* 149:181–186
- Boyce RL, Ocasio M (2020) *Pyrus calleryana* allometric equations and stand structure in southwestern Ohio and northern Kentucky. *Invasive Plant Sci Manag* 13:239–246
- Chapin FS III, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Díaz S (2000) Consequences of changing biodiversity. *Nature* 405:234–242
- Clarke M, Ma Z, Snyder S, Floress K (2019) What are family forest owners thinking and doing about invasive plants? *Landsc Urban Plan* 188:80–92
- Clarke M, Ma Z, Snyder S, Floress K (2017) Private woodland owners and invasive plant management in Illinois. *The Voice for Illinois Forests* 12:17–21
- Connolly BA, Boutiette K (2020) A likely *Pyrus* × *Calleryana* × *Communis* (Rosaceae) hybrid found in Connecticut. *Rhodora* 122:112–113
- Coyle DR, Williams BM, Hagan DL (2021) Fire can reduce thorn damage by the invasive Callery pear tree. *HortTechnol* 31:625–629
- Culley TM (2017) The rise and fall of the ornamental Callery pear tree. *Arnoldia* 74(3):2–11
- Culley TM, Hardiman NA (2007) The beginning of a new invasive plant: a history of the ornamental Callery pear in the United States. *BioScience* 57:956–964
- Culley TM, Hardiman NA (2009) The role of intraspecific hybridization in the evolution of invasiveness: a case study of the ornamental pear tree *Pyrus calleryana*. *Biol Invasions* 11:1107–1119
- Culley TM, Hardiman NA, Hawks J (2011) The role of horticulture in plant invasions: how grafting in cultivars of Callery pear (*Pyrus calleryana*) can facilitate spread into natural areas. *Biol Invasions* 13:739–746
- Dey DC (2014) Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *For Sci* 60:926–942
- Dey DC, Knapp BO, Battaglia MA, Deal RL, Hart JL, O’Hara KL, Schweitzer CJ, Schuler TM (2019) Barriers to natural regeneration in temperate forests across the USA. *New For* 50:11–40
- Díaz S, Lavorel S, de Bello F, Quétier F, Grigulis K, Robson TM (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proc Natl Acad Sci USA* 104:20684–20689
- Drury WH, Nisbet ICT (1973) Succession. *J Arnold Arbor* 54:331–368
- Dunn K (2018) Distribution and Spread of an Invasive Shrub (*Pyrus calleryana*, Decne.) across Environmental Gradients in Southern Indiana. M.S thesis. West Lafayette, IN: Purdue University. 95 p
- Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503–523
- Ehrenfeld JG, Kourtev P, Huang W (2001) Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecol Appl* 11:1287–1300
- Eviner VT, Garbach K, Baty JH, Hoskinson SA (2012) Measuring the effects of invasive plants on ecosystem services: challenges and prospects. *Invasive Plant Sci Manag* 5:125–136
- Farkas A, Orosz-Kovács Z, Szabó L (2002) Insect attraction of flowers in pear cultivars. *Acta Hort* 596:773–776
- Flory SL, Clay K (2010) Non-native grass invasion suppresses forest succession. *Oecologia* 164:1029–1038
- Garnier E, Cortez J, Billès G, Navas M-L, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint J-P (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85:2630–2637
- Gaskin JF (2017) The role of hybridization in facilitating tree invasion. *AoB Plants* 9:plw079
- Gross KL, Emery SM (2007) Succession and restoration in Michigan old field communities. Pages 162–183 in Cramer VA, Hobbs RJ, eds. *Old Fields: Dynamics and Restoration of Abandoned Farmland*. Washington, DC: Island Press
- Hardiman NA, Culley TM (2010) Reproductive success of cultivated *Pyrus calleryana* (Rosaceae) and establishment ability of invasive, hybrid progeny. *Am J Bot* 97:1698–1706
- Harrison XA (2015) A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. *PeerJ* 3:e1114
- Hart JL, Holmes BN (2013) Relationships between *Ligustrum sinense* invasion, biodiversity, and development in a mixed bottomland forest. *Invasive Plant Sci Manag* 6:175–186
- Hartman KM, McCarthy BC (2004) Restoration of a forest understory after the removal of an invasive shrub, amur honeysuckle (*Lonicera maackii*). *Restor Ecol* 12:154–165
- Hartman KM, McCarthy BC (2007) A dendro-ecological study of forest overstorey productivity following the invasion of the non-indigenous shrub *Lonicera maackii*. *Appl Veg Sci* 10:3–14
- Hartman KM, McCarthy BC (2008) Changes in forest structure and species composition following invasion by a non-indigenous shrub, amur honeysuckle (*Lonicera maackii*). *J Torr Bot Soc* 135:245–259
- Hartshorn JA, Palmer JF, Coyle DR (2022) Into the wild: evidence for the enemy release hypothesis in the invasive Callery pear (*Pyrus calleryana*) (Rosales: Rosaceae). *Environ Entomol* 51:216–221
- Hay AE (2021) Leaf phenology and freeze tolerance of the invasive tree *Pyrus calleryana* (Rosaceae) and potential native competitors. Honors thesis. Dayton, OH: University of Dayton. 24 p
- Heemsbergen DA, Berg MP, Loreau M, van Hal JR, Faber JH, Verhoef HA (2004) Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science* 306:1019–1020

- Hermes DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annu Rev Entomol* 59:13–30
- Hobbs RJ (2012) *Old Fields: Dynamics and Restoration of Abandoned Farmland*. Washington, DC: Island Press. 347 p
- Hopkins WE, Wilson RE (1974) Early oldfield succession on bottomlands of southeastern Indiana. *Castanea* 39:57–71
- Jo I, Fridley JD, Frank DA (2017) Invasive plants accelerate nitrogen cycling: evidence from experimental woody monocultures. *J Ecol* 105:1105–1110
- Levine JM, Vilà M, Antonio CMD, Dukes JS, Grigulis K, Lavelle S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. B* 270:775–781
- Liao C, Peng R, Luo Y, Zhou X, Wu X, Fang C, Chen J, Li B (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol* 177:706–714
- Lüdtke D (2021) sjstats: Statistical Functions for Regression Models. R Package Version 0.18.1. doi: 10.5281/zenodo.1284472; <https://CRAN.R-project.org/package=sjstats>
- MacDougall AS, Gilbert B, Levine JM (2009) Plant invasions and the niche. *J Ecol* 97:609–615
- Maloney ME, Hay A, Borth EB, McEwan RW (2022) Leaf phenology and freeze tolerance of the invasive tree *Pyrus calleryana* (Rosaceae) and potential native competitors. *J Torr Bot Soc* 149:273–279
- Marchante E, Kjølner A, Struwe S, Freitas H (2008) Short- and long-term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Appl Soil Ecol* 40:210–217
- Merritt BJ, Jones JB, Hardiman NA, Culley TM (2014) Comparison of photosynthetic characteristics in cultivated and wild offspring of the invasive Callery pear (*Pyrus calleryana* Decne.). *Biol Invasions* 16:393–400
- Morrison J, Mauck K (2007) Experimental field comparison of native and non-native maple seedlings: natural enemies, ecophysiology, growth and survival. *J Ecol* 95:1036–1049
- Niemiera AX (2018) Bradford Callery Pear (and other cultivars). Blacksburg: Virginia Cooperative Extension 3010-1464
- Nowicki M, Huff ML, Staton ME, Trigiano RN (2022) Chloroplast genome of the invasive *Pyrus calleryana* underscores the high molecular diversity of the species. *J Appl Genet* 63:463–467
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020) vegan: Community Ecology Package. R Package Version 2.5-7. <https://CRAN.R-project.org/package=vegan>
- Oosting HJ (1942) An ecological analysis of the plant communities of Piedmont, North Carolina. *Am Midl Nat* 28:1–126
- Pallant E, Riha SJ (1990) Surface soil acidification under red pine and Norway spruce. *Soil Sci Soc Am J* 54:1124–1130
- R Core Team (2020) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org>
- Reich PB (2014) The world-wide “fast–slow” plant economics spectrum: a traits manifesto. *J Ecol* 102:275–301
- Root RA, Wilson RE (1974) Changes in biomass of six dominant plant species during oldfield succession in southeastern Indiana. *Ohio J Sci* 35:370–375
- Sapkota S, Boggess SL, Trigiano RN, Klingeman WE, Hadziabdic D, Coyle DR, Olukolu BA, Kuster RD, Nowicki M (2021) Microsatellite loci reveal genetic diversity of Asian Callery pear (*Pyrus calleryana*) in the species native range and in the North American cultivars. *Life* 11:531
- Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM, O'Connor MI, Rice WR (2007) Ecological and evolutionary insights from species invasions. *Trends Ecol Evol* 22:465–471
- Schierenbeck KA, Ellstrand NC (2008) Hybridization and the evolution of invasiveness in plants and other organisms. *Biol Invasions* 11:1093
- Schulte LA, Mottl EC, Palik BJ (2011) The association of two invasive shrubs, common buckthorn (*Rhamnus cathartica*) and Tartarian honeysuckle (*Lonicera tatarica*), with oak communities in the midwestern United States. *Can J For Res* 41:1981–1992
- Serota TH, Culley TM (2019) Seed germination and seedling survival of invasive Callery pear (*Pyrus calleryana* Decne.) 11 years after fruit collection. *Castanea* 84:47–52
- Shi Z, Liu S, Liu X, Centritto M (2006) Altitudinal variation in photosynthetic capacity, diffusional conductance and $\delta^{13}\text{C}$ of butterfly bush (*Buddleja davidii*) plants growing at high elevations. *Physiol Plant* 128:722–731
- Siemann E, Rogers WE (2003) Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. *J Ecol* 91:923–931
- Simberloff D (2010) Invasions of plant communities—more of the same, something very different, or both? *Am Midl Nat* 163:220–233
- Skurski TC, Rew LJ, Maxwell BD (2014) Mechanisms underlying non-indigenous plant impacts: a review of recent experimental research. *Invasive Plant Sci Manag* 7:432–444
- Sofaer HR, Jarnevich CS, Pearse IS (2018) The relationship between invader abundance and impact. *Ecosphere* 9:e02415
- Soil Survey Staff (2023) Web Soil Survey. Natural Resources Conservation Service, United States Department of Agriculture. <http://websoilsurvey.nrcs.usda.gov/>. Accessed November 27, 2023
- Souza L, Bunn WA, Simberloff D, Lawton RM, Sanders NJ (2011) Biotic and abiotic influences on native and exotic richness relationship across spatial scales: favourable environments for native species are highly invulnerable. *Funct Ecol* 25:1106–1112
- Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. *Trends Ecol Evol* 21:645–651
- US Environmental Protection Agency (2011) Level III and IV ecoregions of the conterminous United States. Corvallis, OR: US EPA, National Health and Environmental Effects Research Laboratory
- Vincent MA (2005) On the spread and current distribution of *Pyrus calleryana* in the United States. *Castanea* 70:20–31
- Ward JS, Williams SC, Linske MA (2018) Influence of invasive shrubs and deer browsing on regeneration in temperate deciduous forests. *Can J For Res* 48:58–67
- Warrick AR, Marshall JM (2018) Callery pear (*Pyrus calleryana*) response to fire in a managed prairie ecosystem. *Invasive Plant Sci Manag* 11:27–32
- Weidenhamer JD, Callaway RM (2010) Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. *J Chem Ecol* 36:59–69
- Wells OO, Schmidting RC (1990) *Platanus occidentalis* L. Sycamore. Pages 1004–1018 in Burns RM, Honkala BH, technical coordinators. *Silvics of North America*. Volume 2, Hardwoods. Agriculture Handbook 654. Springfield, VA: U.S. Department of Agriculture
- Wiedenmann RN (2001) The siege of invasive species in midwestern ecosystems. Pages 1–5 in Proceedings, US Department of Agriculture Interagency Research Forum on Gypsy Moth and other Invasive Species 2001. Newtown Square, PA: US Department of Agriculture, Forest Service, Northeastern Research Station
- Wiken E, Jiménez Nava F, Griffith G (2011) North American Terrestrial Ecoregions—Level III. Montreal, Canada: Commission for Environmental Cooperation
- Woods MJ, Attea GK, McEwan RW (2021) Resprouting of the woody plant *Pyrus calleryana* influences soil ecology during invasion of grasslands in the American Midwest. *Appl Soil Ecol* 166:103989
- Woods MJ, Bauer JT, Schaeffer D, McEwan RW (2023) *Pyrus calleryana* extracts reduce germination of native grassland species, suggesting the potential for allelopathic effects during ecological invasion. *PeerJ* 11:e15189
- Yokomizo H, Possingham HP, Thomas MB, Buckley YM (2009) Managing the impact of invasive species: the value of knowing the density–impact curve. *Ecol Appl* 19:376–386
- Zirbel CR, Bassett T, Grman E, Brudvig LA (2017) Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. *J Appl Ecol* 54:1070–1079