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Article

Rodent-mediated seed limitation affects woody seedling establishment more than invasive shrubs and downed woody debris

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Abstract

Seedling establishment is crucial for the development of self-regenerating tree populations. Determinants of tree establishment vary widely and may compound in their effects. Using a factorial experiment, we manipulated invasive shrubs, downed woody debris (DWD), and rodent access to evaluate factors limiting the establishment of six woody species (five native trees, one invasive shrub). Our results suggest these factors independently contribute to tree seedling establishment. Exclusion of rodents increased establishment threefold. Invasive shrub removal (*Elaeagnus umbellata*; *Lonicera maackii*) and the presence of DWD promoted establishment of two native trees (*Pinus strobus*; *Sassafras albidum*). Notably, the presence of DWD halved *L. maackii* establishment. In identifying rodents as drivers of seed limitation, our results support findings that seed additions will likely promote woody seedling establishment when rodents are not abundant (e.g., low populations) or when seeds are physically or chemically protected (e.g., via taste deterrents). Management plans vary in DWD retention; results from our experimental cohort indicate retaining or introducing DWD promotes native tree recruitment and limits invasive shrub establishment. Future studies exploring the species-specific effects of invasive shrub removal and DWD amendments across multiple cohorts will help determine which woody species benefit most from these management practices.

Key words: tree regeneration, seedling establishment, invasive shrubs, woody debris, seed predators

Introduction

Sustainable forestry requires a mechanistic understanding of how the environment influences tree population regeneration (Vickers et al. 2019*a*, 2019*b*; Piana et al. 2021), generating a constantly evolving challenge for management as regional climates are redefined (Millar and Stephenson 2015). The establishment of tree seedlings—defined as the emergence and persistence of tree seedlings for >1 year (Clark et al. 1999)—is essential for the development of robust and self-regenerating tree populations that shape future forest structure (Hurtt and Pacala 1995; Norghauer and Newbery 2011; McConkey et al. 2012; Forsyth et al. 2015). Given the fundamental role of seedling establishment in determining the dynamics of future forests (Vickers et al. 2019*a*; Piana et al. 2021) and the low potential or regeneration success in many northern temperate U.S. forests (Vickers at al. 2019*b*), it is critical to identifying what and how environmental factors limit or promote early establishment in these forests.

A primary challenge to maximizing tree recruitment is that multiple, diverse, and interacting factors shape tree seedling establishment and survival (Goldberg 1985; Royo and Carson 2006; De Lombaerde et al. 2020; Piana et al. 2021). Competition with overstory trees and vegetation in the subcanopy can lead to light limitation, and this competition is a bottleneck in the development of tree seeds into seedlings (Bolton and D'Amato 2011; Urgenson et al. 2012). Consumption of seeds and seedlings by animals limits juvenile tree seedling establishment and survival (Goldberg 1985; Gill 1992*a*, 1992*b*; Crawley and Long 1995; Zwolak et al. 2010; Boone and Mortelliti 2019), with the potential to influence the trajectory of forest community structure (Hulme and Kollmann 2005; Norghauer and Newbery 2011). Downed woody debris (DWD) modifies forest floor microclimate with context-dependent and species-specific effects on germination and seedling persistence (Harmon et al. 1986; Gray and Spies 1997; Ettinger et al. 2017; De Lombaerde et al. 2020). Complicating matters, these factors rarely operate alone: competition, granivory, herbivory, and microsite limitation co-occur. For example, while invasive shrubs compete for resources with tree seedlings in the forest understory, the presence of these invasive shrubs also correlates with more granivore activity (Dutra et al. 2011; Guiden and Orrock 2019), prolongs granivore foraging time (Mattos and Orrock 2010), results in greater tree seed removal (Bartowitz and Orrock

2016), and alters tree seed consumption and caching near DWD (Guiden and Orrock 2017). While consensus is developing regarding how these ecological factors may independently alter tree seed survival and seedling establishment (e.g., Bartowitz and Orrock 2016; Ettinger et al. 2017), our understanding of regeneration in northern temperate forests will be furthered by empirical evidence examining how these ecological factors may synergistically—or antagonistically—interact to shape juvenile tree survival.

Management is most effective when foresters can act according to the relative importance of constraints on seedling establishment (Webster et al. 2018). To combat competition with invasive shrubs, for example, forests in the midwestern and eastern United States often undergo understory clearing and managers use follow-up control measures (e.g., herbicides) to eliminate these shrubs, restore native forest structure, and promote target seedling establishment (Hartman and McCarthy 2004; Shields et al. 2015; Ward et al. 2018). Foresters may employ unique sowing strategies (e.g., broadcast seed timing, sowing depth) or introduce physical and chemical barriers to overcome seed limitation due to consumption by animals (Willoughby et al. 2011; Leverkus et al. 2015; Löf et al. 2019). Management strategies often recommend introducing or retaining heterogeneity in the forest landscape (e.g., snags, DWD, canopy thinning, and gap generation) to increase the likelihood of suitable microclimates for tree seedling establishment and survival (Gray and Spies 1997; Bolton and D'Amato 2011; Ettinger et al. 2017; De Lombaerde et al. 2020). Employing these techniques requires knowledge regarding whether and how environmental factors interact to shape juvenile tree survival and performance. A strong interaction between two factors, for example, may require a context-specific management strategies that addresses the joint effects. Recommendations to retain or introduce DWD on the forest floor may increase suitable microclimate for seed germination and protection of saplings from ungulate browsing (Whyte and Lusk 2019) but adding DWD concurrently introduces refuge for small mammal seed predators that reduced tree seed survival in certain forest structure (e.g., Schnurr et al. 2004; van Ginkel et al. 2013; but see Ettinger et al. 2017). Experiments are needed that evaluate how different forest understory structures shape the independent and interactive effects of granivores and DWD on tree seedling establishment in temperate mixed deciduous forests.

We use experimental removal of invasive shrubs (i.e., a manipulation of forest understory structure), manipulations of DWD, and exclusion of small mammal granivores to quantify how invasive shrubs, DWD, and rodents may act, alone or in concert, to modify tree seedling establishment in a mixed deciduous northern temperate forest. We focused our study on species that are integral to forest development and management in upper Midwest forests, examining how the removal of invasive shrubs, *Lonicera maackii* (Amur's Honeysuckle) and *Elaeagnus umbellata* (Autumn Olive), affects the recruitment of *Acer rubrum* (Red Maple), *Pinus strobus* (Eastern White Pine), *Quercus rubra* (Northern Red Oak), *Sassafras albidum* (Sassafras), and *Tsuga canadensis* (Hemlock). *Lonicera maackii* and *E. umbellata* are invasive shrubs that negatively affect native trees (Catling et al. 1997; Orrock et al. 2015), and they may limit tree recruitment via competition, by changing small mammal granivory, or both (Orrock et al. 2015). Given that studies have regularly reported more granivory in midwestern U.S. forests invaded by non-native shrubs (Orrock et al. 2010; Bartowitz and Orrock 2016) and rates of tree seed consumption can be greater near DWD (Schnurr et al. 2004; van Ginkel et al. 2013), our experiment is explicitly designed to determine how invasive shrubs in a midwestern U.S. mixed deciduous forest affect how DWD and seed-eating rodents interact to influence tree seedling recruitment. By evaluating multiple, interactive factors that affect tree recruitment, our study will help managers identify conditions in mixed-deciduous forest where recruitment from seed should be highest; our study will also provide an example of whether common management tools (e.g., invasive shrub removal, leaving DWD following harvest) may yield maximum benefit in conjunction with broadcast seed sowing in this forest context.

Methods

Field site

We conducted replicated manipulations of invasive shrub presence at Fish Lake Environmental Education Center (FLEEC), a 240 acre mixed hardwood forest property operated by Eastern Michigan University. Western portions of FLEEC property were historically in agricultural and plantations until the property was acquired by the Eastern Michigan University in 1965, when cultivation of agricultural and wooded lands ceased. The current overstory includes *Q. rubra* and other hardwoods (*Carya ovata*, *Acer* spp.) with associated conifers (e.g., *P. strobus* and *Pinus resinosa*). Invasive woody shrubs encroachment is prevalent in the post agricultural portion of the FLEEC property with the dominant introduced shrubs being *E. umbellata* and *L. maackii*.

In May 2018, we delineated fourteen (14) 20 × 20 m plots and then stratified and paired these plots along a west to east gradient to generate seven blocked plot pairs; the minimum distance separating plots was 50 m. One plot in each block was randomly assigned to have the invasive shrub layer mechanically removed and chemically controlled ("Invaders Removed"), the invasive shrub layer was left intact for the other plot in each block ("Invaders Present"). Prior to invasive shrub removal, we generated size-class distributions of the two dominant invasive shrubs, *L. maackii* and *E. umbellata*, in 5 × 5 m subplots randomly positioned within the larger 20 m × 20 m plot. For 12 of the 14 sites, we measured photosynthetically active radiation (PAR) transmittance (1.25 m height) using a Decagon ceptometer (Decagon Devices, Pullman, WA) at 2 m meter intervals along a linear transect running diagonally through the center of each plot. Ambient PAR measurements were taken simultaneously with a handheld PAR sensor (Decagon Devices, Pullman, WA) to generate estimates of PAR interception at each plot (see Figs. S1A and S1B).

In June 2018, we imposed our "Invaders Removed" treatment. All invasive stems within or overhanging each plot were tagged and then removed mechanically ~5–8 cm above the soil surface using hand tools. Cleared vegetation was evenly distributed >10 m from the plot perimeter to avoid generating unnatural refuges or resources for animals around our plots. Invasive shrub stumps and small invasive shrub growth were chemically treated with glyphosate (Roundup®, Monsanto) immediately after shrub removal and plots were target treated every subsequent October and May from 2018 to 2021 to maintain the invasive shrub removal treatment effect. In July 2018, we estimated PAR transmittance (as described above) to quantify the effects of our invasive shrub removal treatment on light transmittance.

Native tree and exotic shrub seedling establishment

To test the effects of DWD on woody seedling establishment, each plot was divided in half (i.e., "half-plot") and DWD treatment manipulations ("DWD absent" or "DWD present") were randomly assigned to one half of each plot. To generate the DWD absent treatment, DWD was removed from a 2.5 m × 5 m section from the center of the assigned plot half. The removed DWD was relocated to the center of the other plot half and deposited in a loose network covering approximately 2.5 m × 5 m with a maximum height of 30 cm. We made significant effort to match experimental DWD deposit structure to nearby natural DWD amalgamations, with particular emphasis on mainitaining comparable heights and stem density between natural and artificial DWD structures. We standardized our DWD structure as described in similar studies (van Ginkel et al. 2013; see Fig. S2 for representative photos of this treatment) and focused on using DWD only found within the plot to ensure we did not modify the composition (i.e., source species) or the total amount of DWD found on a whole plot.

Consistent with results reported in similar systems, ancillary experiments (Supplemental Data 3) indicate that representative granivore activity is likely lower on shrub-cleared plots relative to invaded plots (Fig. S3A; Connolly et al. 2021) and that the rate of tree seed removal is slower on plots with invasive shrubs removed relative to shrub invaded plots (Fig. S3B). To test the effect of seed predators on woody seedling establishment, we nested two types of exclosures within the center of each DWD half-plot treatment (four total exclosures per plot). One of the exclosures in each half-plot pair excluded small mammal seed predator entry ("Rodents Excluded"), whereas the other exclosure permitted seed predator entry through holes cut in the side of the exclosure ("Rodents Permitted"). In August 2019, we embedded each exclosure 25 cm deep in the mineral soil to prevent small mammals burrowing into the cages. Squares of hardware cloth were secured as lids. To generate the seed predator access treatment, we randomly chose one of the two exclosures on each half-plot half and cut two 5 × 5 cm openings on opposite sides of the exclosure to permit small mammals entry. All exclosures were constructed of 1 × 1 cm hardware cloth secured in a ring with wire cage clips so that the diameter of each exclosure was 15 cm (0.017 m^2 surface area); the small footprint and large mesh size of our exclosure was selected to minimize the effects of exclosure-mediated microclimate modifications on tree seedling establishment (Evans et al. 2018).

On 1 November 2019, seeds of six woody species common on the FLEEC property were sown into each exclosure: Sassafras (*S. albidum*), Red Maple (*A. rubrum*), Canadian Hemlock (*T. canadensis*), Northern Red Oak (*Q. rubra*), Eastern White Pine (*P. strobus*), and Amur's Honeysuckle (*L. maackii*). Seeds of *S. albidum*, *A. rubrum*, *T. canadensis*, and *Q. rubra* were purchased from a commercial vendor (Sawyer Nursery Inc., Hudsonville, Michigan, USA) focusing on seed accessions from upper Midwestern U.S. states. *Pinus strobus* seeds were provided by the Michigan Department of Natural Resources and were sourced from collected accessions from southern Michigan. *Lonicera maackii* seeds were sourced from mature fruit collected from parent plants on the FLEEC property. Prior sowing all *S. albidum*, *A. rubrum*, *T. canadensis*, *P. strobus*, and *L. maackii* seeds were first sorted using firmness, and viability of subsamples was confirmed with cut tests (Karrfalt 2008).*Quercus rubra* seeds were sorted by the float test, and a subset of the acorns were cold stratified for 21 days and their viability was confirmed via a germination test. These tree species are ideal for this study because (1) all study species are found on and around the FLEEC property (Springer and Parfitt 2010; M. Hanes and M.I. Bunker, unpublished data), (2) represent common overstory species found in central and eastern Michigan (Petrides and Wehr 1998), and (3) post-dispersal seed predators forage on these woody species (e.g., Mattos et al. 2013; Bartowitz and Orrock 2016; Guiden and Orrock 2017; Chandler et al. 2020) indicating that we are liklely to detect relationships between seed removal and seedling establishment if these responses are correlated with each other. Ten seeds of each species (only five *Q. rubra* acorns) were sown into each exclosure to mimic low to moderate natural woody plant seed density in the soil (Leckie et al. 2000). Plots were monitored until the cessation of the experiment on 27 May 2021, when we counted final seedling establishment.

Data analysis

We used generalized linear mixed models using Template Model Builder with a binomial distribution to estimate how the independent and interactive effects of invader removal, manipulation of DWD, and seed predator access influenced the proportion seedling establishment 19 months after sowing (i.e., our final seedling establishment estimates). Little to no *Q. rubra*, *A. rubrum*, and *T. canadensis* established across all experimental units (established seedlings: *Q. rubra*, $n = 3$; *T. canadensis*, $n = 2$; *A. rubrum*, $n = 0$), precluding analysis of these species. We ran separate models for the species with establishment (*P. strobus*, *S. albidum*, and *L. maackii*) and the random error structure modeled in our analyses accounted for the split-plot design of experiment; i.e., invasive cover manipulated within block and DWD manipulated within invader treatment plot. Establishment of *S. albidum* was almost exclusively in units excluding granivores, which precluded full model convergence. Consequently, we reduced the structure of the model evaluating *S. albidum* establishment to include invader removal, DWD manipulation, and granivore access as main effects and a single interaction term between invader removal and DWD manipulation. We used R (R Core Team 2022) and associated packages for all statistical analysis and

Table 1. Results from generalized linear models testing for the effect of rodent access, invasive shrub removal, manipulations of downed woody debris, and all possible higher order interaction terms on the proportion of *Pinus strobus* and *Lonicera maackii* seeds that become established seedlings.

Factor	χ^2	Df	*p*-value
Lonicera maackii			
Invaded (INV)	0.85	1	0.355
Downed woody debris (DWD)	3.88	1	0.049
Rodent access (ROD)	11.72	1	<0.001
INV × DWD	0.12	1	0.734
INV × ROD	0.02	1	0.875
DWD × ROD	0.05	1	0.825
INV × ROD × DWD	0.27	1	0.602
Pinus strobus			
Invaded (INV)	2.61	1	0.106
Downed woody debris (DWD)	3.86	1	0.049
Rodent access (ROD)	12.04	1	<0.001
INV × DWD	0.60	1	0.437
INV × ROD	0.23	1	0.630
DWD × ROD	0.76	1	0.384
INV × ROD × DWD	0.30	1	0.586
Sassafras albidum			
Invaded (INV)	4.94	1	0.026
Downed woody debris (DWD)	4.62	1	0.032
Rodent access (ROD)	11.88	1	<0.001
INV × DWD	2.47	1	0.116

Note: Rodent access was tested independently for *Sassafras albidum* establishment because nearly all establishment was in rodent-excluded treatments, precluding the testing of interactions that included this factor. Bolded values indicate that the factor was statistically significant at a type I error = 0.05.

graphics generation: "ggplot2" (Wickham 2016), "car" (Fox and Weisberg 2019), "glmmTMB" (Brooks et al. 2017), "ggpattern" (FC and Davis 2022), and "emmeans" (Lenth 2022).

Results

Across all treatment levels, ~7.7% of sown *L. maackii* seeds established as seedlings. Excluding granivores from sown *L. maackii* seeds resulted in threefold greater *L. maackii* seedling establishment (Table 1; Fig. 1). DWD presence resulted in ~50% less *L. maackii* establishment, but invasive shrub cover did not affect *L. maackii* establishment (Table 1).

Approximately 5.0% of sown *P. strobus* seeds established as seedlings. Excluding granivores from sown *P. strobus* seeds increased *P. strobus* seedling establishment fourfold (Fig. 1, Table 1). Across all treatment levels, the presence of DWD resulted in 2.6 times greater *P. strobus* seedling establishment (Table 1). *P. strobus* seedling establishment tended to greater in plots with invaders removed, but the differences in means between the invasive shrub removal treatments (presence versus removal) was not statistically significant at a Type I error equal to 0.05 (Table 1).

Granviore exclusion resulted in significantly greater *S. albidum* seedling establishment (Table 1). Only 0.4% of *S. albidum* seedlings—one seedling of 280 sown *S. albidum* seeds—established in plots that permitted granivore access, but ~10% of total sown *S. albidum* seeds (29 seedlings total) established in plots that excluded granivores (Fig. 1). Removal of invasive shrubs and the addition of DWD independently increased average *S. albidum* seedling establishment (Table 1). Fourfold more *S. albidum* seedlings established in plots where invasive shrubs were removed than plots where invasive shrubs were left intact; the presence of DWD resulted in over threefold more *S. albidum* seedling establishment than when DWD was removed (Fig. 1).

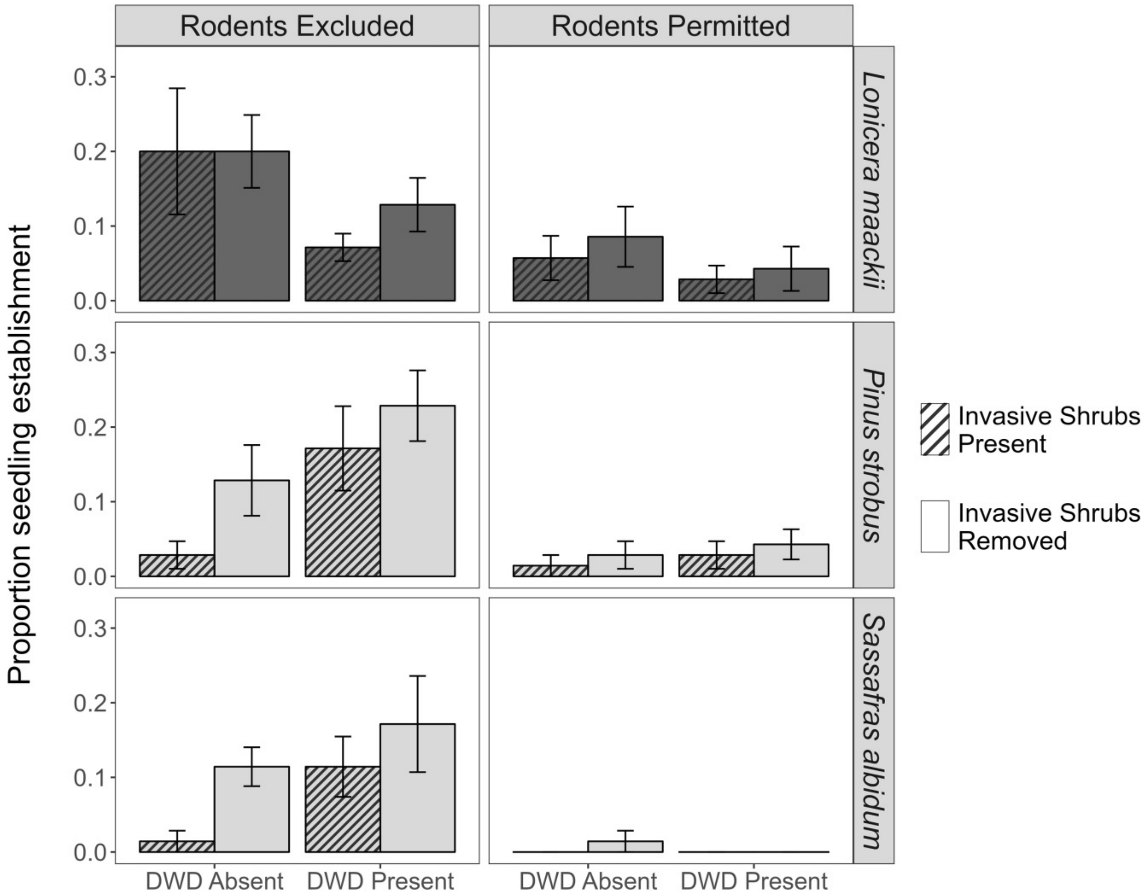
Discussion

Sustainable forest management ultimately requires identifying the factors affecting the establishment of trees from seeds (Webster et al. 2018; Piana et al. 2021). By monitoring seed and seedling fate for 19 months, we gain insight into how multiple factors (i.e., invasive shrubs, native animals, and DWD) can affect the native tree and invasive woody shrub establishment in a mixed deciduous forest. Our study provides insight into the hierarchy of establishment limitations encountered by dispersed seeds of woody plants during our study period: (1) invasive shrubs in the canopy generate species-specific limitations on native tree seedling establishment and have little effect on invasive shrub establishment, (2) DWD promotes establishment of dispersed native seeds and limits invasive shrub establishment, and (3) seed and seedling limitation by granivores results in reductions in native woody plant establishment with similar, but muted, effects on invasive shrub establishment. Importantly, we did not find strong interactions among these three factors during our study, suggesting that in certain forest contexts managers may consider each factor independently when planning management. Our work has two primary implications: (1) ecological barriers vary predictably in how strongly they affect the establishment of tree seedlings in certain years, and (2) forest context prior to reforestation (e.g., presence of invasive shrubs, DWD coverage, small mammal populations) could generally inform the likelihood of successful seedling establishment from natural seed rain or from reforestation using seed additions.

Ecological barriers to tree seedling establishment

Invasive shrubs introduce significant interspecific competition in forest understories (Gorchov and Trisel 2003; Orrock et al. 2015), but the effects of invasive shrubs on the establishment of woody species may be species-specific (Fig. 1; Gorchov and Trisel 2003; Urgenson et al. 2012). Several mechanisms may explain why the positive effects of invasive shrub removal differed in magnitude between *S. albidum* and *P. strobus*. Native species response to invasive shrub removal may correlate with the degree of shade tolerance: *S. albidum* is intolerant of shade, whereas *P. strobus* has intermediate shade tolerance (Burns and Honkala 1990). Invasive plants removal promotes rapid growth in seedlings of early seral trees, but shade-tolerant trees can display a muted response to this

Fig. 1. The effect of manipulating invasive shrub cover, downed woody debris (DWD), and mammalian seed predator access on the establishment (i.e., emergence and survival after 19 months) of an invasive shrub species (*Lonicera maackii* (Amur Honeysuckle); dark gray columns) and two native tree species (*Pinus strobus* (Eastern White pine) and *Sassafras albidum* (Sassafras); light gray columns); columns represent means ± standard error.



same treatment (Urgenson et al. 2012). Low seed addition density may also contribute to low *P. strobus* establishment in invasive shrub removal plots. Fewer potential germinants in each exclosure increases the likelihood that stochastic factors may swamp signals associated with the invasive shrub treatment. Our seed addition density (~2650 seeds m^{-2}), however, aligned with the ranges reported in naturally occurring temperate forest seed banks (Leckie et al. 2000, and references therein) and limits the potential to overestimate the effects seed predation. Finally, seed predator activity was comparable between invasive shrub treatment plots in Fall 2019 (Fig. S3) suggesting granivory may have been similar between the invasive shrub treatment plots during the year seeds were sown. Our work provides a detailed examination of how one experimental cohort responds to these ecological barriers, but empirical evaluations of potentially interacting factors shaping tree seedling establishment (e.g., granivory exclusion and invasive shrub removal) may be most informative when seed additions are repeated and monitored over multiple, successive years.

DWD is a common feature of forest floors (Harmon et al. 1986). Greater DWD density can correspond to greater tree seedling establishment (Schnurr et al. 2004), but the effects of DWD on seedling establishment may be species-specific. DWD halved *L. maackii* seedling establishment and the effect of DWD on *L. maackii* establishment was cumulatively greater when the invasive shrub understory was intact (Fig. 1). Light attenuation by both canopy and understory vegetation (Fig. S1B) and DWD (Gray and Spies 1997) may limit photosynthesis, pushing *L. maackii* below its physiological limits in forest interiors (e.g., light compensation point; Lieurance and Landsbergen 2016), increasing soil moisture (Gray and Spies 1997; Roberts et al. 2005), and lowering seed survival by facilitating soil pathogens that grow in darker, damper soils (Taher and Cooke 1975; Augspurger 1990; Orrock et al. 2012). For native woody species, however, DWD promoted seedling establishment (Fig. 1). Native tree seed germination and seedling survival can be greater on or around DWD collections (Gray and Spies 1997; O'Hanlon-Manners and Kotanen 2004; Kupferschmid and Bugmann 2005). DWD can diminish air and soil temperature extremes and increase soil moisture (Roberts et al. 2005; Goldin and Hutchinson 2013; Dhar et al. 2022), which can foster tree seedling survival (Harmon and Franklin 1989; Gray and Spies 1997) and buffer tree seedling growth in dry years (Roberts et al. 2005). Currently, it is unclear what mechanisms resulted in the divergent responses we observed for native versus invasive woody species establishment, but the joint manipulation of invasive plant cover and DWD can promote woody seedling survival in certain forest contexts (e.g., urban forests, Ettinger et al. 2017). We did not, however, detect strong interactive effects between these factors in this mixed deciduous forest during our study period suggesting that interannual climate trends or other factors (e.g., forest position along a rural-to-urban gradient; Ettinger et al. 2017) may alter the degree to which different environmental factors shape tree regeneration from seeds.

Exclusion of seed-consuming animals, predominantly white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*; see Supplementary Data 3), generated a nearly ubiquitous increase in woody seedling establishment. Seed consumption is a well-documented barrier to tree seedling establishment (Gill 1992*a*; Zwolak et al. 2010), with the potential to decrease basal area production and slow tree population growth (Norghauer and Newberry 2011; Forsyth et al. 2015). Sown seeds may have been dispersed to caches (Vander Wall et al. 2005), but we observed few to no seedlings emerging outside our cages on plots and none of the seedlings we did observe were clumped together suggesting germination of a cache (B. Connolly, personal observation). Notably, seed consumption contributed to minimizing honeysuckle establishment suggesting granivores can play a role minimizing invasive shrub recruitment (i.e., biotic resistance), although magnitude of granivory's effect on invasive plant establishment will depend on propagule pressure (Davis 2009) and the extent to which habitats differ in invasibility (Connolly et al. 2014). Granivory undoubtedly shaped seedling establishment in this mixed deciduous forest during this study period, underscoring the importance of long-term monitoring of tree seed additions to determine how exclusion of granivores translates to forest productivity.

Limitation by inadequate microsite conditions, nontarget biotic agents, or adverse edaphic conditions likely influenced test species establishment and precluded significant establishment three of our five native tree species. For example, when rodents were excluded, *P. strobus* and *S. albidum* establishment was low when invasive shrubs were present and DWD was absent (Fig. 1), suggesting that adverse environmental conditions (e.g., greater temperature extremes, low soil water content) drove low establishment for these two species on invader present plots. Importantly, the presence of DWD appears to ameliorate these poor establishment conditions, resulting in a more than threefold increase in establishment on shrub invaded plots for these species. *Quercus rubra* acorns only remained intact in exclosures that excluded seed predators; however, only three of the 180 intact acorns in rodent exclusion plots emerged as seedlings despite >80% viability at the experiment's sow date. This result suggests that the environmental conditions manipulated in our study (e.g., invasive shrub cover, DWD manipulation) did not promote *Q. rubra* establishment, and other environmental factors not directly manipulated in our study (e.g., edaphic conditions, invertebrate predation) limited native tree recruitment. For example, Raynal et al. (1982) demonstrate that low substrate pH can limit the *A. rubrum* and *T. canadensis* germination, although soil pH estimates for our study plots (Supplementary Data 4) did not reach the low pH levels used in their study. Winter conditions or invertebrate granivores and herbivores can also drive low seed survival for *A. rubrum* and *T. canadensis* in Midwestern U.S. forests (Chandler et al. 2020; Guiden and Orrock 2021). For example, consumption by small invertebrates (e.g., earthworms, mollusks) that could still access the added tree seeds in rodent exclosures may have compensated for experimentally excluded small mammal seed predators (Harper 1977; Cassin and Kotanen 2016), by minimizing post-emergence woody plant seed and seedling survival and effectively forestalling recruitment for *A. rubrum* and *T. canadensis* (B. Connolly, unpublished data). Our study demonstrates that tree seedling establishment is the product of multiple and diverse environmental factors and while our study helps rank predominant ecological filters to tree seedling establishment, other environmental factors (e.g., climate extremes) will also contribute to limitation and may need to be accounted for in management approaches for different forest contexts.

Management strategies targeting tree seedling establishment

Our work provides empirical support that certain forest management practices increase tree seedling establishment. Broadcast seed sowing, for example, may be an effective means of promoting tree seedling establishment, but only if steps are taken to minimize the effects of herbivores and competition with other vegetation (Willoughby et al. 2004; Overdyck et al. 2013; Löf et al. 2019). Seed addition often promotes seedling establishment and managers may consider how the timing of seed additions, such as during different seasons (Radvanyi 1970; Tilki and Alptekin 2006), will minimize the effects of granivores on tree seedling emergence. Rodent population abundance often varies dramatically from year to year (Sullivan et al. 2023), such that adding seeds during times of low rodent abundance, or when rodents are sated due to masting events, may increase seedling recruitment (Schnurr et al. 2004). Coating broadcast seeds in repellents may similarly be an effective means of deterring seed consumers (Willoughby et al. 2011); naturally occurring compounds (e.g., capsaicin) may be an effective means of deterring seed predators and some in restoration systems suggests the effects of seed coat deterrents can promote target plant establishment (Pearson et al. 2019; Lanni et al. 2023). When seeds are protected from rodents or sown during a time when there is likely to be less granivory, targeting seed broadcasting on or around naturally occurring collections of DWD may simultaneously promote tree seedling establishment and protect developing seedlings and saplings from larger herbivores (van Ginkel et al. 2013; Whyte and Lusk 2019).

Invasive shrubs can contribute to limitation in native tree regeneration and, consequently, invasive shrub control would contribute to restoring natural tree regeneration (Ward et al. 2018). Our work corroborates the practice of invasive shrub removal as it leads to overall average increases in native seedling establishment 19 months after treatment, although this effect may be most apparent in early seral

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woody species such as *S. albidum* (Fig. 1). Ward et al. (2018) demonstrated long-term effects of invasive shrub removal by reporting increases in native tree seedling density persisting 9 years after invasive shrub removal; interestingly, seedlings <30 cm tall of large-seeded native trees (e.g., *Quercus* sp., *Carya* sp., *Acer* spp., *Prunus serotina*) recruit to higher densities in invasive shrub removal plots in this study suggesting that environmental factors known to act strongly on larger seeded species (e.g., granivory) may be less potent when invasive shrubs are mechanically removed.

Managing to retain or increase local aggregations of DWD will also likely facilitate seedling recruitment. Our work supports the retaining of DWD on plots cleared of invasive shrubs for two reasons. First, we observed greater seedling establishment for both *P. strobus* and *S. albidum* on plots with DWD present. Second, we observed that invasive *L. maackii* seedling establishment was significantly lower in the presence of DWD. The dual potential to increase regeneration of desirable native trees while curtailing the recruitment of invasive woody plants may be an elegantly passive strategy to restore natural regeneration or promote growth of target tree species during reforestation. Site-level characteristics of DWD (e.g., composition, volume, and density) may alter seed predators' activity and foraging (Sullivan et al. 2012; Malo et al. 2013; Guiden and Orrock 2021). Consequently, examining how differing densities and characteristics of the DWD drive these divergent patterns across different forest contexts is an important next step to securing this practice as a management objective in shrub-invaded forests.

Conclusions and future directions

Managing tree seedling establishment from seed can promote sustainable forest production initiatives but requires a comprehensive understanding of a forest's environmental context to be effective. We have demonstrated that recruitment of native species to tree seedling stage can be promoted through limiting the effects of granivores, targeting seed sowing on or around aggregations of DWD, and removing the invasive shrub layer. While we have demonstrated the potency of these environmental constraints to limit seedling establishment, longer term studies are needed to track how these factors link to the generation of healthy and robust adult trees. Describing seedling establishment is an essential first step towards regeneration, but the fate and structure of future forests will also be a function of how ecological factors shape longer term tree demography and growth (Norghauer and Newbery 2011; Forsyth et al. 2015; Royo and Carson 2022). For example, while invasive shrubs had a small effect on seedling establishment of *P. strobus*, persistent habitation underneath invasive shrubs is also likely to negatively affect native tree seedling and sapling survival and growth in subsequent years (Fagan and Peart 2004) suggesting this management approach may play a more significant role in *P. strobus* regeneration at older life stages. Tree seedling establishment is variable across time (Clark et al. 1999). Given several species failed to recruit following seed additions under any experimental conditions and given we only examined the establishment of one experimental cohort, our study also highlights the importance of examining how other factors such as broader forest context (e.g., rural vs. urban forests, land-use history) or limitation by invertebrate consumers and pathogens in the soil (O'Hanlon-Manners and Kotanen 2004; Cassin and Kotanen 2016) may contribute to tree seedling establishment across time. Ultimately, healthy forests must regenerate and actively, informed participation in the process of promoting tree seedling establishment is a significant step to ensure that management practice meets sustainability goals on forested land.

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Data availability

Data generated or analyzed during this study are available in the DRYAD repository (https://doi.org/10.5061/dryad.69p8cz91t).

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Competing interests

The authors declare that there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfr-2023-0131.

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