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Undesirable woody establishment is driven by herbaceous cover phylogenetics and abiotic conditions

Rolando Trejo-Pérez[1,2] · **Pierre-Luc Chagnon**[1,3] · **Béatrice Gervais-Bergeron**[1] · **Patrick Boivin**[1] · **Jacques Brisson**[1]

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Abstract

Revegetation with herbaceous covers is widely employed to inhibit tree encroachment in managed areas. However, most studies have focused on species selection for inclusion in herbaceous seed mixtures, neglecting the effect of local contingencies such as soil conditions and native vegetation emerging from the seed bank. Here, we tested the potential of sown herbaceous seed mixtures and local site conditions to reduce the abundance and establishment of three undesirable woody species. We sowed herbaceous seed mixtures containing 3, 5, or 8 species in a recently cleared right-of-way. Over two consecutive years, we allowed spontaneous vegetation establishment. We measured three facets of its diversity: taxonomic, functional, and phylogenetic. We also evaluated how woody encroachment was spatially structured and influenced by soil physicochemical properties. Our findings show that herbaceous seed mixtures were poorly established, hence they did not significantly impact overall seedling establishment. We also observed that no "silver bullet" mechanisms effectively inhibit the establishment of multiple woody species. The inhibition of woody species also involved multiple mechanisms, with phylogenetic diversity metrics being the dominant predictors of tree encroachment in the first year. However, the significance of abiotic mechanisms intensified in the second year. This temporal shift added complexity to identifying the most effective vegetation management strategies for inhibiting invasive and undesirable species. Our study illustrates how successful revegetation strategies for inhibiting tree species should account for herbaceous seed mixture effectiveness under ideal conditions and ecological versatility (i.e., the ability of these species to regenerate and thrive in various soil types and climatic conditions). Hence, effective prevention of woody species establishment on bare soil sites linked to infrastructure projects necessitates a multifaceted approach that integrates sown plant diversity and a comprehensive understanding of soil properties and resident vegetation diversity.

Keywords Revegetation · Community assembly · Functional diversity · Woody colonization · Woody encroachment

Introduction

Revegetation can be a useful technique in ecosystem management, which can be used in controlling soil erosion, improving landscape aesthetics, creating new habitats for biodiversity conservation, or even controlling undesirable and alien species (Isbell et al. 2011; Burt 2012). Revegetation using herbaceous cover species, for example, is a widely employed approach to mitigate the adverse environmental effects of infrastructure projects that often involve vegetation removal. Notable examples include the revegetation of downhill ski areas (Burt 2012) and pipeline or electrical powerline rights-of-way (Shatford et al. 2003; Yannelli et al. 2017; Motti et al. 2020). In such cases, revegetating bare soils serves multiple purposes, including preventing soil erosion (Chen et al. 2015; Crouzeilles et al. 2016; Peng and Li

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✉ Rolando Trejo-Pérez
rolando.trejo.perez@umontreal.ca

[1] Institut de Recherche en Biologie Végétale, Université de Montréal, 4101 Sherbrooke St E, Montreal, QC H1X 2B2, Canada

[2] Present Address: Université TÉLUQ, Université du Québec, 5800 Saint-Denis St, Montreal, QC H2S 3L4, Canada

[3] Present Address: Agriculture and Agrifood Canada, Saint-Jean-Sur-Richelieu RDC, 430 Boulevard Gouin, Saint-Jean-Sur-Richelieu J3B 3E6, Canada

2017), promoting plant community diversity (Bullock et al. 2011; Liu et al. 2008; Moreno-Mateos et al. 2012; Gornish et al. 2017), and enhancing landscape aesthetics (Breed et al. 2013). Additionally, revegetating bare soils prevents site colonization by nonnative species or, more broadly, possibly undesirable species such as trees (MacDougall et al. 2009). In such a context, when the objective is to prevent the establishment of certain species, applied vegetation management has substantially borrowed from theoretical and empirical progress made in invasion ecology and community assembly theory more broadly (e.g., Case 1990; Chase and Myers 2011; Hess et al. 2019; Hooper & Dukes 2010; Frankow-Lindberg 2012; Rauber et al. 2013).

Several mechanisms influence how easily non-native (or native, but undesirable) plants establish in a new area. These can include propagule pressure (von Holle & Simberloff 2005; Waddell et al. 2020), temporal or spatial windows of resource availability (Davis et al. 2000; Grace et al. 2017; Davies et al. 2005; Belote et al. 2008), and interactions with neighbors (Levine & D'Antonio 1999). The latter can include niche-based explanation based on trait and/or phylogenetic proximity to resident species (e.g., St. Clair et al. 2016; Gerhold et al. 2015; Byun et al. 2020), or indirect biotic such as apparent competition driven by shared enemies (e.g., Orrock et al. 2008). However, in the context of applied revegetation for infrastructure projects, they traditionally focus on designing species mixtures for establishment on bare soils to prevent invasion by undesirable species (Balandier et al. 2006; Byun et al. 2012; DeSandoli et al. 2016). This emphasis often overlooks the role of spontaneously emerging species from the local seed bank, which can contribute significantly to the resident community composition (Schuster et al. 2017; Bramble et al. 1996; Brown 1995; de Blois et al. 2004; Flory and Clay 2010; Desrochers et al. 2020). Most controlled studies evaluating the relationship between resident community alpha diversity and the probability of being invaded/colonized frequently involve the removal of spontaneously emerging species through weeding (Hooper & Dukes 2010). These controlled studies are often conducted in homogeneous environments, carefully controlling for site heterogeneity through randomization and blocking techniques of their experimental designs. Therefore, the results from such diversity-invasion experiments poorly reflect natural revegetation contexts (Grace et al. 2016; Veen et al. 2018). While controlled common garden studies are essential for isolating the role of plant species composition and/or diversity, there is a significant knowledge gap regarding the impact of spontaneous vegetation regeneration and local site heterogeneity as potential drivers of site colonization by undesirable species. This gap includes the simultaneous influence of microenvironments, availability of light, soil properties such as soil nutriments (Bonebrake et al. 2011; Foster et al. 2002), spatially structured propagule rain from unwanted species (Cadotte et al. 2008; Flynn et al. 2011), community composition such as the effectiveness of native seed additions to rehabilitate or restore species composition (Foster et al. 2015; Grman et al. 2013) on natural and semi-natural ecosystems, and the relationships of native-exotic species (Bassett et al. 2024).

Revegetation of bare soil under electrical power line rights-of-way is a particular example where revegetation of bare soil is required and where the inhibition of unwanted species is targeted. These sites serve as a practical context for applied vegetation management, where the joint consideration of herbaceous seed mixtures and other endogenous site factors (space, soil, and resident plant community) is crucial. The revegetation of these systems often faces the challenge of tree establishment, which can pose risks to infrastructure integrity and maintenance operations (de Blois et al. 2004; Hill et al. 1995; Mercier et al. 2001; Shatford et al. 2003; Turk et al. 2017). Tree colonization via the right-of-way after soil clearance is highly likely to depend on local contingencies such as spatially heterogeneous propagule rain (depending on the proximity of seed trees belonging to different species) or soil properties that may be linked to local variations in texture or microtopography. Clearing operations in rights-of-ways are also expected to lead to rapid reassembly of a ruderal plant community from the seed bank. Tree establishment and growth in these systems may thus depend not only on herbaceous seed mixture diversity but also on the combined diversity of both sown and naturally regenerating species. Although the use of preselected herbaceous species has shown promising results in inhibiting woody species in controlled experiments (e.g., Brown 1995; de Blois et al. 2004; Flory & Clay 2010; Trejo-Pérez et al. 2024), additional work is required to determine the role of local drivers, including soil properties and spontaneous vegetation.

In a recent study, we tested the effectiveness of various herbaceous seed mixtures as blocking agents against the establishment and growth of two undesirable tree species, namely red maple (*Acer rubrum* L.) and gray birch (*Betula populifolia* Marshall). These two species are often abundant in powerline corridors in Northeastern North America, leading to costly maintenance efforts to keep a low vegetation cover (Boivin et al. 2018). Under controlled conditions, we examined the relative contributions of composition (species identity) and diversity (taxonomic and functional) of herbaceous seed mixtures. We found that the identity (presence or absence) of specific herbaceous species, particularly *Achillea millefolium* L. and *Solidago canadensis* L., better predicted the resistance of resident herbaceous seed mixtures to tree encroachment than mixture diversity per se (Trejo-Pérez et al. 2024). Here, building upon these findings, we conducted a field experiment to assess the effectiveness of these herbaceous seed mixtures under realistic field conditions while also considering local site factors such as soil properties, spatial patterns, and the alpha diversity (taxonomic, functional, phylogenetic) of the resident plant community. Over two consecutive years, we closely monitored tree colonization in our plots. We hypothesized that tree establishment would exhibit a negative correlation with the species richness of our herbaceous seed mixtures. We also hypothesized that woody encroachment would exhibit a negative correlation with resident community alpha diversity (taxonomic, functional, and phylogenetic), a positive correlation with bare soil and plant-available nutrients, and spatial aggregation due to potential spatial autocorrelation in unmeasured soil properties, herbaceous regeneration from the seed bank and tree propagule rain.

Materials and methods

Field experiment

Overview of the experiment

We conducted a field experiment in a recently cleared right-of-way in the park Pointe-aux-Trembles Montreal, Canada (45° 41′ 36.1288″ N and 73° 30′ 46.9519″ W). The climate is continental and characterized by cold winters, heavy snowfall, and hot, humid summers. The growing season varies from 120 to 140 days (Environment Canada 2022), with a mean annual precipitation of 988 mm and a temperature of 6.5 °C. The soil is sandy with minor gravel (Prest & Hode-Keyser 1975). The average soil pH is 6.6, with relatively little organic matter (3.9%, measured by loss on ignition). Before May 2020, several established woody species colonized this right of way. *Rhamnus cathartica* L., *Acer negundo* L., and *Robinia pseudoacacia* L. represented 98.5% of the woody species. In May 2020, a forestry shredder was used to remove previously sampled vegetation. All the roots found within the first 30 cm of the soil profile were removed with a shredder, which was passed over a 72 m × 30 m band. This operation involved mixing the soil and the roots of the vegetation present in our study site, probably resulting in a nutrient flush. The 72 m × 30 m band was then separated into three 24 m × 30 m experimental blocks. These plots were further subdivided into 3 subplots (8 m × 30 m), resulting in 9 experimental plots. In May 2020, the day after the shredder operation, one of three herbaceous seed mixtures was sown in each plot (Appendix S1).

Herbaceous seed mixture selection

We designed three herbaceous seed mixtures (3, 5, and 8 species), manipulating the diversity of companion species to include *Solidago canadensis* L. and *Achillea millefolium* L. These two species were found to be efficient in inhibiting tree seedling establishment and growth ((Trejo-Pérez et al. 2024). We selected the companion species among *Poa pratensis, Festuca rubra, Agrostis gigantea, Trifolium repens,* and *Lotus corniculatus* L. These companion species are common naturalized grassland species in the study area and their seeds are readily available from commercial suppliers. In all our herbaceous seed mixtures, we also included *Lolium multiflorum* Lamarck, which serves as a fast colonizer of bare ground, quickly establishes and blocks undesirable species the first year, and leaves room for other sown species to become dominant the year after. This priority effect is well recognized in revegetation studies (D'Antonio & Meyerson 2002; de Blois et al. 2004). Table 1 details the composition of the herbaceous seed mixtures. We tested the germination rates of all the species before the experiment, and all the species had germination rates above 55%, except for *S. canadensis*, which had 27 seedlings per each gram of mulch (Table 1).

Field data collection

In each of our 9 experimental plots, we established 6 quadrats (2 m × 1 m) at the center of the 8 m × 5 m experimental plot subdivisions. In September 2020 and 2021, we conducted surveys in these quadrats to gather data on the established seedlings from our tree invaders. To avoid dependent variable autocorrelation over time, we counted only the

Table 1 Composition of herbaceous seed mixtures for the revegetation plan under the electrical power rights-of-way approach

Species	Mixtures (%)			Seeding rate (g/m^2)	Germination (%) ± standard error
	M1	M2	M3		
Solidago canadensis L.	14.3	25	50	42*	27.3 ± 9.2*
Achillea millefolium L.	14.3	25	50	1	98.3 ± 1.6
Trifolium repens L.	14.3	25		1	98.7 ± 0.8
Lotus corniculatus L.	14.3	25		0.9	94.2 ± 2.2
Poa pratensis L.	14.3			12	59.7 ± 5.9
Festuca rubra L.	14.3			32	87.5 ± 3.7
Agrostis gigantea Roth	14.3			8	65.3 ± 4.0

*27.3 ± 9.2: It corresponds to the number of seedlings germinated in 1 g of mulch. In a gram of mulch there are on average 6416 ± 333.6 seeds

The mixture percentage is based on the total herbaceous seed weight mixture. The same seeding rate (1 g/m^2) of *Lolium multiflorum* was used for all the mixtures. The percentage of *L. multiflorum* germination in the laboratory was 97.2 ± 1.0%. An asterisk (*) indicates that for *S. canadensis*, because separating and weighing individual tiny seeds was impractical, we weighed and sowed a mulch on crushed ripe inflorescences, so the mass is reported as g of mulch/m^2

seedlings that were established within each year. Seedling age was estimated by counting terminal bud scars. In the same quadrats, we also estimated plant percent cover based on a semiquantitative scale following Mercier et al. (2001). We divided the percent cover into eight classes: 0–1%, 1–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–100%, and 100%. We used the median value of each class cover to assign a plant cover value to each quadrat. We also determined the proportion of bare soil, and we collected one soil sample per plot (54 soil samples) to determine physical and chemical properties. The soil samples were air-dried in the laboratory following the Li et al. (2020a, b) methodology. Soil moisture and temperature were determined as the average of several readings using a TDR-150 probe. Light levels were measured with a Fisher brand traceable dual-display light meter.

Laboratory analysis

Soil properties

In addition to the field-collected data, we used soil samples to determine several soil properties directly associated with plant nutrition. For this purpose, we determined (1) pH, measured by soaking soil in a mixture of one part soil to two parts water using a benchtop pH meter; (2) KCl (2 N)-extractible mineral nitrogen, determined following the methodology described by Jones & Willett (2006) and Kranabetter et al. (2007) to extract and quantify the mineral nitrogen content; (3) Mehlich-III-extractible orthophosphate, determined using the Mehlich-III extraction method and the molybdenum blue colorimetric assay as described by Sauer & Meek (2003); and (4) organic matter (%) content, determined by loss on ignition following the protocol outlined by Powlson et al. (2013) (Appendix S2).

Data analysis

Functional diversity

We calculated indicators of functional diversity to determine whether tree establishment was more likely to occur in communities of functionally similar resident/sown species (Appendix S2). In addition to species richness (SR) and functional group richness (FGR), we determined functional richness (FRic), evenness (FEve), divergence (FDiv), and dispersion (FDis) as well as Rao's quadratic entropy (Q) (RaoQ) using the R package FD (version 1.0-12.1; Laliberté et al. 2023). We constructed a matrix of the relative herbaceous cover as a proxy for species abundances, and we targeted traits linked to different organs of the plants (Yannelli et al. 2017). We considered 12 traits: mycorrhizal type, seed dry mass (mg), leaf phenology type, plant growth form, plant lifespan (longevity), bloom season, fruit type, leaf type, reproduction type, plant life form (Raunkiaer life form), maximum plant height generative and vegetative (m), and leaf area per leaf dry mass (specific leaf area, SLA or 1/LMA) ($mm^2 mg^{-1}$). We gathered trait information for all species, 46 in 2020 and 59 in 2021, from the TRY (Kattge et al. 2019) and FungalRoot (Soudzilovskaia et al. 2020) databases. If some traits were not available directly from these databases, we searched them in the literature to find specific trait information. All trait information can be found at https://doi.org/10.5683/SP3/XP9HLG.

Phylogenetic diversity

We computed phylogenetic community alpha diversity metrics using the R package picante (version 1.8.2; Kembel et al. 2020). To do so, we first constructed a phylogenetic tree by pruning the supertree included in V.PhyloMaker (version 0.1.0; Qian and Jin 2016; Jin and Qian 2019), which contains > 70,000 species (available at https://github.com/jinyizju/). For genera or species in our dataset that were absent from the supertree, we added them to their respective families (in the case of genera) and genera (in the case of species) in the megaphylogeny using Scenario 3, which is analogous to using Phylomatic with Bladj to generate a phylogeny (Webb et al. 2008). We constructed a phylogenetic tree from the mega tree “GBOBTB.extended”, which we subsequently converted to Newick format. We calculated the phylogenetic diversity (PD), mean nearest taxon distance (MNTD), mean pairwise distance (MPD), phylogenetic species variability (PSV), clustering (PSC), richness (PSR), and evenness (PSE) (Miller et al. 2017). For all calculations, we considered the relative abundances of the species by using the recorded percent cover as a proxy (Appendix S2).

Spatial analyses

We used Moran's eigenvector maps (MEMs) following Dray et al. (2012) to control potential spatial autocorrelation in unmeasured environmental properties, seed rain, and remaining vegetative propagules that may contribute to woody encroachment. We used the ade4 (version 1.7-22; Dray et al. 2023a, b) and adespatial (version 0.3-23; Dray et al. 2023a, b) R packages. This approach designs orthogonal (independent) spatial vectors that could be used as predictors of woody encroachment in our downstream statistical analyses (see below).

Statistical analyses

To assess the effectiveness of herbaceous mixtures and explore potential mechanisms driving woody encroachment, we employed two distinct statistical approaches.

These analyses aimed to address our initial research question regarding the impact of herbaceous mixtures on woody species encroachment. Additionally, they were designed to investigate various factors beyond the herbaceous seed mixtures themselves, including spatial, soil, and vegetation mechanisms contributing to woody encroachment.

Herbaceous seed mixtures effect

To analyze the effect of herbaceous seed mixtures on woody encroachment, we employed generalized linear mixed models (GLMMs) with Poisson or binomial negative distributions. We used the lme4 (version 1.1-31; Bates et al. 2023), dplyr (version 1.1.3; Wickham et al. 2023a, b), and ggplot2 (version 3.4.2; Wickham et al. 2023a, b) R packages. We focused our analyses on the three prominent species established at our site, namely, *Acer negundo* L., *Robinia pseudoacacia* L.*,* and *Rhamnus cathartica* L.. We built regression models for each tree species individually using the number of seedlings present in each quadrant as the response variable. To further examine the significant differences among the 3 herbaceous seed mixtures used in this experiment, we constructed a model using herbaceous seed mixture identity as a predictor (M1, M2, and M3: see Table 1) of seedling abundance for each woody species individually, and we included the block as a random effect (3 blocks). We aggregated data from quadrats inside each of our experimental plots (9 mixture lines). We subsequently conducted mean comparisons as post hoc tests using the emmeans (version 1.8.4-1, Lenth et al. 2023) R package.

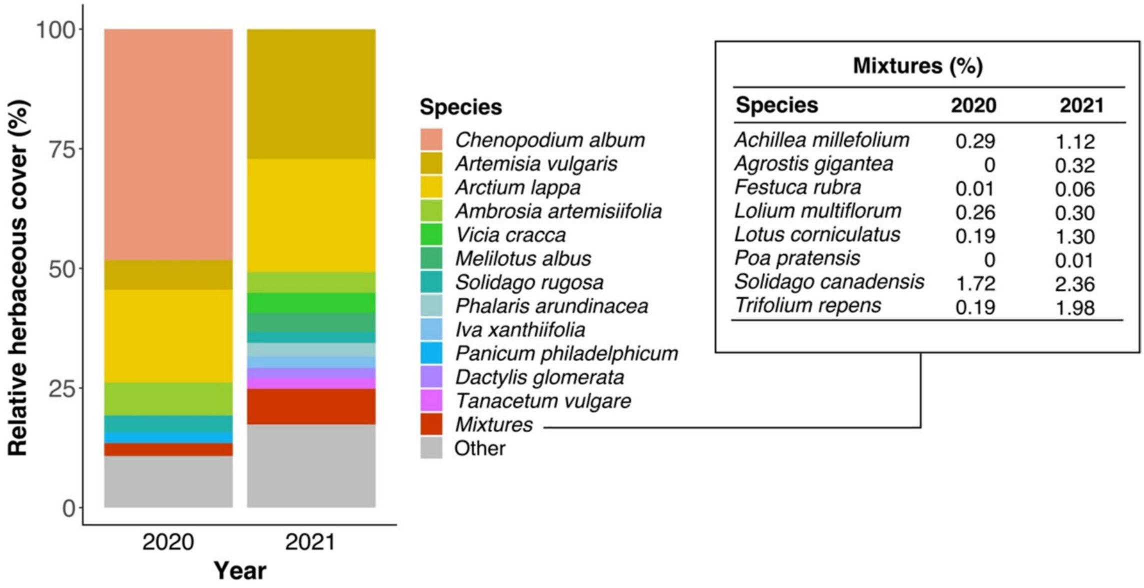
Multiple mechanism effect

To further explore the relative contributions of space (MEMs), soil properties, and vegetation (i) taxonomy, (ii) function, and (iii) phylogenetic diversity to tree encroachment, we constructed generalized linear models with Poisson and negative binomial distributions or Hurdle models when tree seedling occurrence was very sparse. Before conducting model selection, we explored potential collinearity (thus redundancy) among our predictors. We used the MASS (version 7.3-58.2; Ripley et al. 2023), pscl (version 1.5.5; Jackman et al. 2023), and vegan (version 2.6-4; Oksanen et al. 2022) R packages. Many facets of functional or phylogenetic diversity can be considered potentially redundant to one another (Miller et al. 2017). Similarly, a given soil property gradient could be strongly spatially structured and aligned with a given Moran spatial eigenvector. We visualized covariance among our predictors using principal component analysis (PCA) and retained the 30 most relevant predictors for the construction of PC1 and PC2 using the FactorMineR (version 2.7; Husson et al. 2023) and factoextra (version 1.0.7; Kassambara & Mundt 2020) R packages. We then further eliminated collinear predictors using the variance inflation factor (VIF), removing predictors with a VIF exceeding 5 using the pedometrics (version 0.12.1; Samuel-Sosa et al. 2022) R package (Miller et al. 2017, Appendix S3, S4 & S5). Such prefiltering and removal of redundant predictors are essential for preventing model overfitting, especially in cases such as ours, where the number of observations n is relatively limited ($n = 54$ plots). Backward model selection, as implemented in the step function of the stats (version 4.2.1; R Core Team 2022) package in R, was then employed to determine the main predictors for the final model, and the Akaike information criterion (AIC) was used as the selection criterion (Aho et al. 2014). The predictor coefficients were visualized using the sjPlot R package (version 2.8.12.; Lüdecke 2023). Because tree occurrences were very sparse for some species-year combinations, we wanted to determine how sensitive our model coefficient estimates were to specific data points. We thus conducted a sensitivity analysis by (1) running several iterations of our model with randomized tree occurrences and (2) generating random subsamples (95%) or our full dataset using bootstrapping.

Results

Plant composition

The herbaceous seed mixtures exhibited poor establishment during the first and second growing periods (Fig. 1). This was likely due to the exceptionally dry weather that prevailed in 2020 and 2021, with 28% and 36% less precipitation occurring between May and September, respectively, compared to the average precipitation for that time of year (Appendix S6). The final plant composition of the herbaceous cover community included 46 and 56 species in September 2020 and 2021, respectively. However, the relative herbaceous cover of species from the herbaceous seed mixtures was minimal, accounting for only 2.7% in 2020 and 7.5% in 2021 (Fig. 1 and Appendix S7). Consequently, the final composition was assembled mainly by resident species emerging from the seed bank. *Chenopodium album* L. and *Arctium lappa* L. were the most abundant species in 2020, representing 67.6% of the herbaceous cover. In 2021, *Arctium lappa* L. and *Artemisia vulgaris* L. were the most abundant species, representing 50.7% of the total relative herbaceous cover (Fig. 1). Regarding woody species, approximately 9 seedlings/m^2 were established in 2020, decreasing to 2 seedlings/m^2 in 2021. The main woody species were *A. negundo*, *R. pseudoacacia* and *R. cathartica*. *R. pseudoacacia* was the most abundant species in 2020, while *A. negundo* was more abundant in 2021 (Fig. 2).



Mixtures (%)

Species	2020	2021
Achillea millefolium	0.29	1.12
Agrostis gigantea	0	0.32
Festuca rubra	0.01	0.06
Lolium multiflorum	0.26	0.30
Lotus corniculatus	0.19	1.30
Poa pratensis	0	0.01
Solidago canadensis	1.72	2.36
Trifolium repens	0.19	1.98

Fig. 1 Relative plant cover (%) of species established in the first and second years of revegetation at the experimental site. Mixtures: Herbaceous seed mixtures. These included *Achillea millefolium*, *Lolium multiflorum*, *Lotus corniculatus*, *Trifolium repens*, *Poa pratensis*, and *Festuca rubra*. Other include species with a relative herbaceous cover of less than 2%

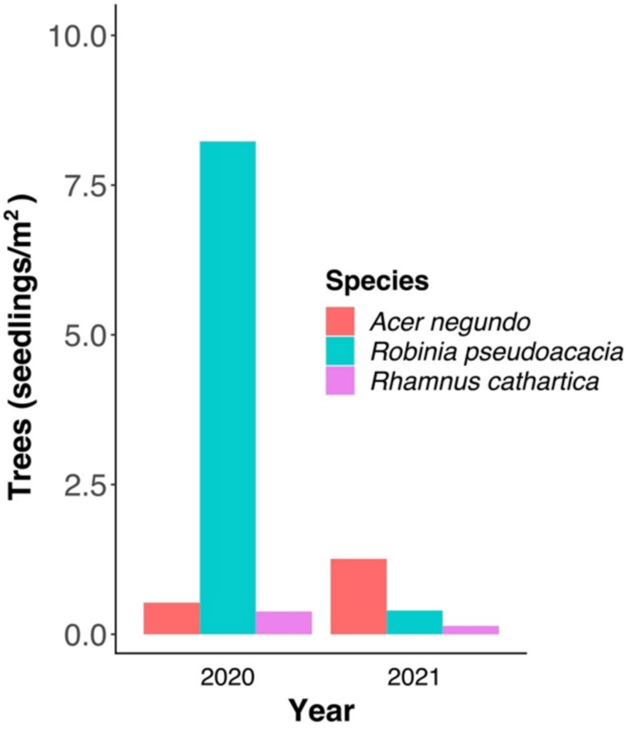


Fig. 2 Woody abundance of undesirable species established in 2020 and 2021. Both 2020 and 2021 included only 1-year-old seedlings

Mechanisms determining woody resistance

In our experiment, we observed no significant effect of the herbaceous seed mixtures on overall seedling establishment, except for *R. pseudoacacia* in the first year. Specifically, the M3 herbaceous seed mixture, consisting only of *S. canadensis*, *A. millefolium,* and *L. multiflorum*, appeared to be slightly less effective at limiting the emergence of *R. pseudoacacia* seedlings in 2020 (Appendix S8).

As a result, model selection rarely retained the herbaceous seed mixture as a predictor of woody seedling establishment; instead, tree seedling abundances were predicted by vegetation functional and phylogenetic diversity metrics in 2020 and mainly by soil abiotic properties in 2021. However, these drivers exhibited inconsistency across tree species or years (Fig. 3). This lack of consistency does not appear to be due to the sparse occurrence of tree seedlings in our dataset; the identities of the selected predictors were highly consistent across our sensitivity analyses with bootstrapped subsamples of our dataset. Moreover, bootstrapped occurrences resulted in widely different predictors being retained during model selection, supporting the idea that our retained predictors indeed have significant predictive power for woody establishment (i.e., they were unlikely to arise as type I errors) (Appendix S9). Finally, in the vast majority of cases, the overall model coefficient of determination (R^2) was significantly greater when using the original data than when shuffling occurred. The only exceptions were *R. cathartica* in 2020 and *A. negundo* and *R. pseudoacacia* in 2021, where models could achieve similar predictive power even on randomized data. These results correspond to year*species combinations in which very few seedlings were recorded, indicating that additional data may be necessary to

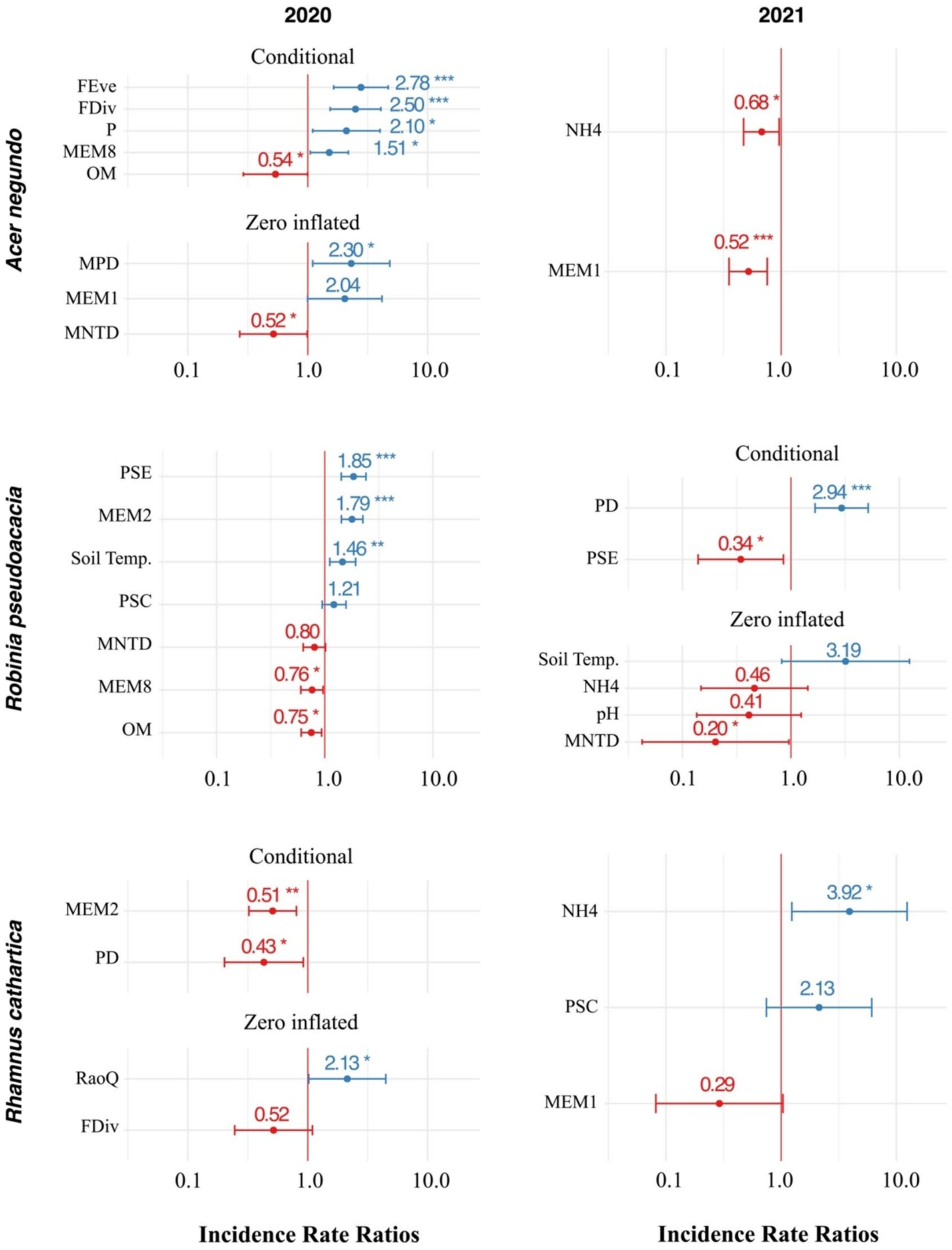


Fig. 3 Incidence rate ratios of woody encroachment vs spatial, abiotic, phylogenetic, and functional mechanisms. Estimates placed on the right of the line of the null effect indicate that an increase in the predictor is associated with an increase in tree abundance (inhibition by a positive relationship). Estimates placed on the left of the line of the null effect indicate that an increase in the predictor is associated with a decrease in tree abundance (inhibition by a negative relationship). The conditional and zero-inflated models correspond to a two-part Hurdle model. Significance codes: 0 "***" 0.001 "**" 0.01"*" "0.05" "0.1" 1. *Acer negundo* 2020 ($R^2=0.55$) and 2021 ($R^2=0.0.18$); *Robinia pseudoacacia* 2020 ($R^2=0.61$) and 2021 ($R^2=0.44$); *Rhamnus cathartica* 2020 ($R^2=0.40$) and 2021 ($R^2=0.31$)

more confidently identify drivers of seedling establishment for these species (Appendix S10).

Herbaceous cover diversity

Considering the final vegetation composed by both the species from seed mixtures and vegetation established spontaneously, in 2020, facets of resident community alpha diversity explained woody establishment, whereas they were largely absent from models in 2021. Interestingly, taxonomic diversity (i.e., species richness) was not retained once in the final models. Instead, the functional and phylogenetic diversity of the herbaceous covers played a crucial role; however, they exhibited variation among woody species over the years of this experiment.

Among the primary functional metrics, we identified three crucial drivers of woody inhibition, and these effects were primarily observed in 2020. Specifically, low functional evenness values were significantly associated with *A. negundo* seedling inhibition in 2020. Similarly, low RaoQ values were significantly linked to the inhibition of *R. cathartica* seedlings. In contrast, functional divergence was negatively correlated with the *A. negundo* seedling number but positively correlated with the *R. cathartica* seedling number (Figs. 2 and S9).

The most influential drivers of woody inhibition in 2020 were related to the phylogenetic diversity of resident vegetation. However, the importance of different phylogenetic diversity metrics varied among woody species. For instance, a low mean pairwise distance (MPD), indicative of high alpha phylogenetic diversity, was associated with fewer *A. negundo* seedlings in 2020, while low phylogenetic species clustering (PSC) (indicating low mean species relatedness) was associated with the inhibition of *R. pseudoacacia* in 2020 and *R. cathartica* in 2021. Similarly, a high mean nearest taxon distance (MNTD) was associated with *A. negundo* and *R. pseudoacacia* inhibition in 2021. However, phylogenetic species evenness (PSE) exhibited contrasting patterns, with low PSE values (indicating that individuals tended to be more related to each other) associated with a greater number of *R. pseudoacacia* seedlings in both 2020 and 2021. The phylogenetic diversity (PD) was also inconsistent across species; it was positively correlated with *R. cathartica* seedlings in 2020 but negatively correlated with *R. pseudoacacia* seedlings in 2021 (Fig. 3 and Appendix S11).

Soil properties

Soil properties played a notable role in woody species establishment during the study, with their significance ranging from poor predictors in 2020 to somewhat essential predictors in 2021. Resource availability, however, had mixed effects on woody establishment. For instance, in 2021, mineral nitrogen was positively associated with *R. cathartica* but negatively associated with *A. negundo.* Additionally, low soil temperatures were a significant driver for restraining *R. pseudoacacia* establishment in 2020 and 2021. Surprisingly, in 2020, high organic matter levels were negatively associated with *A. negundo* and *R. pseudoacacia* establishment. Furthermore, a higher pH was negatively associated with the number of *R. pseudoacacia* seedlings in 2021 (Fig. 3 and Appendix S11).

Spatial patterns

MEM1, MEM2, and MEM8 were the most influential in shaping the spatial structures. However, their effects were contingent on the specific woody species under investigation and exhibited temporal variation over the two years of the study. Low MEM1 values tended to be negatively associated with *A. negundo* seedlings in 2020, while high MEM1 values tended to be negatively associated with both *A. negundo* and *R. cathartica* seedlings in 2021. In contrast, in 2020, low MEM2 values were significantly negative associated with *R. pseudoacacia* seedling abundances, while high MEM2 values were significantly negative associated with *R. cathartica* seedlings. On the other hand, high MEM8 values were negatively associated with *R. pseudoacacia* seedlings in 2020 (Fig. 3 and Appendix S11). In addition, MEM1 was parallel to the forest, along the east–west axis, while MEM2 was orthogonal to the forest and strongly correlated with the distance to the forest border.

Discussion

In the context of a revegetation project, establishing successful herbaceous cover using preselected species composition is highly desirable (de Blois et al. 2004). However, throughout this study, the low germination and establishment of our sown species prevented a robust test of our first hypothesis, which stated that a more diverse herbaceous seed mixture would more efficiently block tree establishment in our plots. Additionally, our findings did not support our second hypothesis about "silver bullet" mechanisms effectively inhibiting the establishment of multiple woody species. We observed that woody inhibition drivers exhibited dynamic variability rather than remaining consistent over time. They were also dependent on the target species, occasionally showing opposite trends across certain species-year combinations. Nevertheless, we identified phylogenetic diversity and abiotic conditions as key factors inhibiting woody species, with phylogenetic diversity as the dominant factor of tree encroachment in the first year, and abiotic conditions taking precedence in the second year.

Understanding the facets of herbaceous vegetation diversity in seminatural ecosystem revegetation

When establishing successful herbaceous covers in seminatural ecosystems, the role of herbaceous seed mixtures is a critical consideration. Many controlled studies have shown that preselected herbaceous covers are highly effective at inhibiting woody species through resource preemption, chemical interference and/or spill-over effects (Bramble et al. 1996; Brown 1995; de Blois et al. 2004; Flory & Clay 2010). In this study, a primary purpose was to test the efficiency of preselected herbaceous seed mixtures for limiting the establishment and growth of tree plants (Trejo-Pérez et al. 2024) under realistic field conditions. However, the exceptionally dry springs of 2020 and 2021 were detrimental to the germination and establishment of our sown species, which led our experimental plots to be 97% dominated by resident species instead of by sown species. As a result, we did not find that the diversity of herbaceous seed mixtures influenced woody establishment in our plots.

These findings strongly suggest the necessity of reevaluating the inclusion criteria when developing mixtures intended to control vegetation in managed areas. Traditionally, these mixtures have been assembled based on two primary factors: (1) the availability of seeds on a large scale (de Blois et al. 2004; Stott et al. 2010) and (2) preliminary controlled typical garden trials that demonstrate the efficiency of a subset of commercially available species in suppressing undesirable species (e.g., Trejo-Pérez et al. 2024). The consecutive dry seasons experienced in our study indicate the importance of considering the ecological versatility of species in the selection process. This approach is particularly crucial given that the establishment of herbaceous seed mixtures is a critical first step in effectively blocking undesirable species. Furthermore, as these mixtures are usually designed for application across diverse ecosystems characterized by varying climates, wind patterns, soil types, and fertility levels, incorporating versatile, generalist herbaceous species could improve their efficacy in establishing diverse systems (Stott et al. 2010). For instance, if our herbaceous seed mixtures included exceptionally drought-tolerant species, germination rates and/or survival upon germination might have significantly improved.

The well-established spontaneous vegetation observed in this study also presents an opportunity to explore a new pool of species to consider as potential candidates for revegetation plans. For example, this study revealed that the final vegetation was primarily composed of spontaneous herbaceous species, indicating that the former species are more adaptable to prevailing environmental conditions than the latter species. These opportunistic species tend to exhibit early successional traits, enabling them to quickly occupy bare ground (de Blois et al. 2004; Schuster et al. 2017). The dominance of spontaneous vegetation highlights the need to reconsider how these species thrive under exceptional environmental conditions and integrate the resilience mechanisms involved. This could also enhance our further species selection criteria.

Furthermore, the success of our revegetation efforts could have been enhanced by utilizing alternative sowing methods, such as integrating seeds with a top layer of water-retaining compost or superabsorbent polymers or by providing irrigation during the initial weeks of the experiment (Stott et al. 2010; Auestad et al. 2016; Abella et al. 2015). This approach, however, may not always be feasible in remote field applications. Overall, improving mixture sowing methods can also play a crucial role in determining the success of selected herbaceous seed mixtures as effective agents for blocking undesirable tree species.

No "silver bullet" generally inhibits woody establishment

When considering the impact of resident herbaceous community diversity (taxonomic, functional, and phylogenetic), soil properties, and space, we observed few (if any) consistent trends: the retained predictors were consistent neither across years nor across woody species and sometimes even influenced woody establishment in opposite directions. This highlights the multifaceted and temporally variable influence of environmental properties, spatial dynamics, and plant cover composition on tree establishment (Shea & Chesson 2002; Stotz et al. 2016; Mazía et al. 2019). This complicates any of our attempts to determine the most effective vegetation management strategies for inhibiting invasive and undesirable species (Grace et al. 2017; St. Clair et al. 2016; Schuster et al. 2017; Byun et al. 2020). Moreover, identifying "silver bullet" mechanisms that effectively inhibit the invasion of multiple woody species can prove challenging for ecologists and land managers (Webster et al. 2006). Here, phylogenetic diversity metrics in 2020 and soil properties in 2021 were the factors that significantly explained woody inhibition. We observed these mechanism trends at the local scale, and further research conducted on larger scales and longer periods (greater than three years) (McCallum et al. 2018) would be beneficial for informing land managers of broader applications and implications (Appendix S4). Another limitation of the present study was the sparse occurrences of tree species under study: accurately identifying the drivers of tree establishment will require further data collection over time, and across additional sites.

Functional diversity

Various facets of herbaceous community diversity played a role in inhibiting woody establishment in 2020. Taxonomic diversity, however, was never retained in the final models, contrary to the vast literature on the diversity-invasion relationship (Hooper et al. 2005; St. Clair et al. 2016). Depending on the specific values of functional evenness, functional divergence, and RaoQ, different tree species were either favored or inhibited due to competition or facilitation from the herbaceous community. The effects of functional diversity metrics also did not always support the niche saturation assumption, whereby high functional diversity would better prevent invasions via more complete occupancy/exploitation of available niches (Mason et al. 2005; Renault et al. 2022). For example, in 2020, *A. negundo* was more effective in plots with low functional evenness. The plots were likely dominated by a small subset of species with similar functional traits, suggesting that *A. negundo* seedlings may have suffered from competition with these dominant species (Villéger et al. 2008). Consistent with this, *A. negundo* also demonstrated greater success in plots with high functional divergence, which may suggest that plots with lower functional divergence were dominated by functionally similar, stronger competitors (Kissick et al. 2018). On the other hand, in the same year, high functional divergence seemed to inhibit *R. cathartica* seedlings. Low RaoQ values could suggest reduced taxonomic diversity and the dominance of a few closely related herbaceous species (Larentis et al. 2022), which could create conditions that are less favorable for the establishment of *R. cathartica* seedlings (See species traits similarity in Appendix S12). Additionally, the weak influence of functional metrics in this experiment may be due to the use of international database values, which omit local adaptation. Species often exhibit plastic traits in response to community interactions and site heterogeneity (Albert et al. 2011; Callaway et al. 2003), and along their development (i.e. seedlings vs mature trees) (Cornelissen et al. 2003). Local trait measurements could have provided a better explanation of the local mechanisms implied in tree encroachment.

Phylogenetic diversity

Phylogenetic diversity metrics also played a significant role in influencing woody establishment in our experiment. However, the effects of phylogenetic diversity are contingent upon the specific metrics used, the woody species under consideration, and the temporal dynamics. Initially, we expected more phylogenetically diverse herbaceous communities to inhibit colonization by woody plants (Webb et al. 2002; Mazel et al. 2016; Ernst et al. 2022). Nonetheless, we find no support in some of our phylogenetic metrics assessed. For example, low MPD values of herbaceous communities were associated with less *A. negundo* seedling abundances in 2020, suggesting that an herbaceous community composed of closely related species better competed against *A negundo*. Conversely, low PSC values (indicative of lower phylogenetic dispersion) inhibited the establishment of *R. pseudoacacia* and *R. cathartica* seedlings in 2020 and 2021, respectively. This implies also that closely related herbaceous species appear to inhibit the woody species. We also found mixed support among the phylogenetic metrics assessed. When PSE values were low, suggesting an uneven distribution of phylogenetic diversity, they appeared to inhibit *R. pseudoacacia* seedlings in 2020 but led to the opposite effect on *R. pseudoacacia* seedlings in 2021. This suggests that *R. pseudoacacia*'s response to phylogenetic diversity is intricate and can fluctuate between years. The same is true for phylogenetic diversity per se (Faith's PD; Mazel et al. 2016), in which high PD values inhibited *R. cathartica* seedlings in 2020 and indicated greater phylogenetic diversity. In contrast, low PD values inhibiting *R. pseudoacacia* seedlings in 2021 suggested reduced phylogenetic diversity. However, our trends are aligned with the mixed results support found in the literature regarding whether more phylogenetically diverse communities are less or more invaded (Cavender-Bares et al. 2009; El-Barougy et al. 2020; Galland et al. 2019).

Our phylogenetic diversity results also argue against the idea that better niche saturation through phylogenetic diversity and/or dispersion is key to limiting further plot colonization. Instead, it seems that particular traits that may be phylogenetically conserved are involved in competition against woody seedlings. However, contrary to this argument, higher phylogenetic dispersion (high mean nearest taxon distance, MNTD) seemed to inhibit the establishment of *A. negundo* and *R. pseudoacacia* seedlings in 2020, as well as *R. pseudoacacia* seedlings in 2021. Our result patterns then contrasted with those in invasion-resistance experiments described by Ernst et al. (2022) and (2023), who found that greater phylogenetic diversity may lower resistance to invasion. Overall, our results about phylogenetic signal do not allow us to determine any firm relationships between phylogenetic diversity or dispersion and plot encroachment by woody seedlings; in some cases, seedlings are better established in low-diversity plots (in line with the diversity-invasibility hypothesis), but in others, seedlings are better established in plots with high diversity and/or dispersion, indicating that low-diversity/dispersion plots may harbor closely related, stronger competitors that better block woody seedling establishment. To add further complexity to this, effects could even be reversed within woody species across years.

Soil properties

The results regarding bare soil and plant-available nutrients were also inconsistent regarding their influence on woody encroachment. Although soil properties emerged as the strongest predictors of woody establishment in 2021, we did not find unilateral support for the hypothesis that woody seedlings would thrive in nutrient-rich, warmer soils (Grace et al. 2017). This year, the soil properties exhibited diverse spatial patterns and variations within our experiment, while bare soil was more homogenous across our quadrats. Additionally, plant community species richness correlated with specific soil properties, such as soil temperature and pH, indicating that the herbaceous plant community was not necessarily the primary factor influencing the success of woody species. While *A. negundo* was more abundant in phosphorus-rich plots in 2020, its abundance decreased in nitrogen-rich plots (and remained unaffected by phosphorus) in 2021. Soil pH, which exhibited a negative correlation with distance to the forest border at our site (see Appendix S5), had only a minor effect on seedlings, showing a counterintuitive negative impact on *R. pseudoacacia* in 2021, despite *R. pseudoacacia* not being known for its preference for acidic soils (Cierjacks et al. 2013). In contrast, inhibition related to ammonium resource availability was associated with specific preferences among woody plants in the second year of this experiment. Overall, contrary to several tightly controlled experiments with strong resource gradients or contrasts (e.g., Going et al. 2009), our field study strongly argues against abiotic resistance as a strong predictor of woody seedling colonization or invasion in open fields.

Spatial patterns

Spatial patterns were determined by a few MEMs, capturing the broadest spatial scale patterns, meaning that *A. negundo*, *R. pseudoacacia,* and *R. cathartica* abundances presented a moderately clustered distribution. However, the spatial distributions were inconsistent across years, suggesting that this cannot be merely ascribed to, for example, the distribution of seed trees in the adjacent forest. In the context of tree encroachment dynamics in rights-of-way, it has been observed that the relation between nearby bordering trees, seeds, and seedling abundances can vary among tree species and time (Boivin et al. 2018). In our experiment, we observed different woody spatial distribution patterns attributed to the spatial eigenvector values. For example, the spatial eigenvector MEM1 was directly parallel to the forest border and highly correlated with soil temperature, suggesting that its effect may reflect either the direct impact of temperature on seedlings (Watt & Bloomberg 2012) or the impact of unmeasured soil properties that may covary with temperature (e.g., soil redox potential and nitrification rates). The spatial eigenvector MEM2 showed a high correlation with border distance, and notably, its impact was limited to 2020. That year, *R. pseudoacacia* preferentially established near the forest border, while the opposite was true for *R. cathartica*. This contrast is interesting because both species disperse over short distances (Knight et al. 2007; Cierjacks et al. 2013). In MEM8, clumped seedling distributions were observed (Appendix S13). However, it was not correlated with any variable assessed in this study, meaning that it could capture another spatial structure or relationship (e.g., propagule pressure, unmeasured soil properties, drainage, and microtopography) that is relevant to *R. pseudoacacia* encroachment in semi-natural ecosystems.

Unmeasured environmental variables and indirect effects

Our findings also indicate promising future directions. Despite our predictor's selection criteria and the tests for multicollinearity giving confidence that selected explanatory variables are indeed likely to be of great importance for predicting woody abundances, the associations or patterns observed in our data might not necessarily indicate that one variable is directly causing the other. Instead, these patterns could also be the result of variables being related to another variable, unmeasured variables, or simply coincidental associations. The entire plant community, including both herbaceous and woody species, may be influenced by underlying environmental variables not examined in this study. For example, soil properties, microclimatic conditions, or spatially structured propagule rain could be significant factors that were not explicitly measured but might have contributed to the observed dynamics (Linders et al 2019; Li et al. 2020b). These unmeasured variables could indirectly create conditions that favor or inhibit woody seedling establishment through their influence on the herbaceous community. Future research questions may explore these complex interactions by incorporating a broader range of environmental variables and exploring their direct and indirect effects on both herbaceous and woody species. Additionally, experimental designs that manipulate these environmental factors alongside plant community composition would provide stronger evidence for causal relationships.

Redefining revegetation strategies to inhibit woody encroachment

Improving the selection of species mixtures for revegetation plans with multiple purposes, especially if the goal is to inhibit woody species, has posed challenges for ecologists and land managers (de Blois et al. 2004; Flory & Clay 2010). Redefining strategies require land managers to consider the efficacy of herbaceous seed mixtures beyond ideal conditions and the ecological versatility of the species mixtures selected (Stott et al. 2010; Trejo-Pérez et al. 2024). This becomes even more critical as the performance of herbaceous covers can vary depending on the targeted woody species and temporal variation in mechanisms. Overall, our study underscores the varying impacts of woody encroachment on space, soil properties, and resident vegetation diversity (taxonomic, functional, and phylogenetic). Spontaneous diversity played a compensatory role, quickly occupying the bare soil and effectively offsetting the low success rate of the preselected herbaceous seed mixtures during our exceptionally dry growing seasons. However, predictors of woody establishment were not the same across species and even varied from year to year within species. Rather, we identified phylogenetic diversity and abiotic conditions as key factors in inhibiting woody species. This highlights the need for further research documenting longer-term trends and exploring additional mechanisms not assessed in this study (e.g., further soil properties contributing to abiotic resistance), which can contribute to a better understanding of the ecological versatility of herbaceous species in response to climatic variations. In addition, our findings suggest that promising seed mixes should include species that demonstrate resilience and adaptability across a variety of environmental conditions, such as those capable of thriving in diverse soil types and climatic scenarios. This approach will help create more robust and effective revegetation strategies in semi-natural ecosystems that can better inhibit undesirable tree species.

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Data availability The data that support the findings of our study are openly available via Borealis, the Canadian Dataverse Repository, at https://doi.org/https://doi.org/10.5683/SP3/XP9HLG.

Declarations

Competing interest The authors declare no competing interests.

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