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Avoid, tolerate, or escape? Native vegetation responses to invasion vary between functional groups

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Abstract

Biological invasions are one of the greatest threats to biodiversity and ecosystem functioning. However, the constraints imposed by the invaders on native organisms and their associated response, remain poorly understood. Native species can survive invasion through multiple resistance strategies (avoidance, tolerance, or escape), but the relative importance of each strategy and how they vary among functional groups have been little explored.

In this study, we examined the resistance strategies of native forbs and graminoids facing invasion by Solidago canadensis. First, we characterized the general impacts of invader density on native plant biomass production and diversity. Then, we investigated specific constraints linked to the invasion (competition for light, nutrients and mycorrhizal fungi), and the associated resistance strategies of native species.

S. canadensis had different negative impacts on native vegetation biomass production and diversity – depending on functional groups – due to increased competition for light, nutrients, and mycorrhizal interactions. The increased competition for light was partially (i) avoided (tall forbs and graminoids) or (ii) tolerated (small, shade-resistant graminoids). The effects of (iii) allelopathic compounds and (iv) increased competition for nutrients were avoided by some forbs (high mycorrhizal infection rates). Finally, some forbs and graminoids (v) escaped all constraints by completing their cycle early in the season.

Our results highlight the diversity of non-exclusive strategies (avoidance, tolerance, escape) by which different functional groups can respond to invasion-induced constraints. They suggest that to improve understanding of the mechanisms underlying invasion, the native community responses should be decomposed into strategies specific to functional groups.

Key words: plant invasions, resistance strategies, competition, allelopathy, mycorrhiza, functional traits, diversity indices, community weighted mean.

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Introduction

Invasive plants are known to alter native plant communities and their functions in an ecosystem through a variety of mechanisms (Vilà et al. 2011; Pyšek et al. 2012; Castro-Díez et al. 2016). They are often strong competitors for resources (Gioria and Osborne 2014), can affect biogeochemical cycles (Zhang et al. 2019), arthropod and mycorrhizal communities (Litt et al. 2014; Yuan et al. 2014; Davis et al. 2018), and the interactions of these groups with the native vegetation (Albrecht et al. 2014). Through these mechanisms, they may jeopardize the functioning of the entire ecosystem (Gordon 1998; Vilà et al. 2011).

The constraints exerted by an invader alter resource availability (e.g., light, water, soil nutrients, pollinators, mycorrhizal fungi) and filter native plants depending on their ability to resist these constraints (Stotz et al. 2019). Such filtering modifies the composition, structure and functioning of the community. These changes can be described by summary indices of taxonomic and functional diversity, and biomass production. Community-level metrics provide broad measures of changes. However, they do not help to identify the mechanisms underlying the changes, nor to understand why some native species are more resilient to invader constraints than others (Gallien and Carboni 2017).

Native plant species can employ three possible strategies to resist invasion: avoidance, tolerance, and escape (Figure 1) (Levitt 2015; Yıldırım and Kaya 2017). Little is known about the relative importance of the three strategies to allow persistence in the face of invasion, although these strategies are well known regarding other stresses such as drought (Bodner et al. 2015; Volaire 2018). The *avoidance strategy* refers to native species with sufficiently good abilities to acquire the resources they need regardless of the invader presence (e.g., being tall if the constraint is on light interception, Craine and Dybzinski 2013). The *tolerance strategy* refers to species requiring limited amounts of resources to complete their life cycle (e.g., shade tolerant species, Valladares and

Niinemets 2008). Finally, the *escape strategy* refers to species completing their critical developmental stages before the invader starts its annual development (temporal niche differentiation, Huang et al. 2019). Escape may alter the temporal pattern of floral resources for pollinators (Moroń et al. 2018), while avoidance or tolerance can alter biogeochemical cycles and the likelihood of establishment of other invasive species (Cavieres 2021). In addition, within the same community, different strategies may be deployed by different species in response to the same constraint. To better understand the long-term consequences of invasion on biodiversity and ecosystem functioning, we need to identify and quantify the relative importance of different native species strategies.

Changes in the functional traits of native vegetation can reveal the constraints they experience during invasion and the strategies by which some of the native plants resist these constraints. For each invasion constraint, only the native species that are able to cope with the constraint – by avoiding, tolerating or escaping it – will remain in the community (filtering effects). This will leave a signature in the functional trait space of native species specific to both the constraint and the selected resistance strategi(es). For instance, tall species may avoid competition for light, so an increase in native plant height after invasion may reveal a selection for species with a light competition avoidance strategy. By filtering out native plant species unable to resist invasion-induced constraints, invasive plants can alter the community weighted mean (CWM) of functional traits, as well as decrease or increase their variance (CWV) (via filtering toward one strategy or selecting for different strategies (Sodhi et al. 2019)). Traits’ CWM and their comparison to the invader’s traits are commonly used and can detect trait displacement in the invaded community, but they still fail to detect the existence of different strategies within the community. Therefore, traits’ CWM and CWV should be used together to detect the diversity of strategies that permit some of the native plants to resist the new constraints brought by the invader.

The lack of studies considering the variations of species responses across functional groups also prevents a better understanding of the impact of invasive plants on native vegetation. The vegetation is often considered as a homogeneous assemblage of species, whereas different functional groups (e.g., forbs, graminoids and N-fixers; (Blondel 2003; Münkemüller et al. 2014)) have different development and foraging strategies. For instance, graminoids are more wind pollinated and resistant to herbivory than forbs, and forbs and graminoids have different acquisition systems for some minerals (Marschner 1995). They thus experience different constraints and can respond differently to a biological invasion (Fenesi, Vágási, et al. 2015). Studying the different responses of native functional groups to invasion, in particular regarding resistance strategies, should provide a better understanding of their responses and of the consequences on the ecosystem.

In this study, we characterized the impacts of *Solidago canadensis* (L., 1753) on native plant communities and the mechanisms underlying these impacts in recently colonized (less than 50 years old) French wet meadows encompassing a broad invasion gradient. *S. canadensis* one of the most invasive plants in European and Asian wet meadows (Weber 1998; Morales and Traveset 2009). In experimental conditions, it is able to alter the native plant community through (i) competition (Fenesi, Geréd, et al. 2015), (ii) changes in soil nutrients (Zhang et al. 2009; Scharfy et al. 2010), and (iii) production of allelopathic compounds that affect native species interactions with arbuscular mycorrhizal fungi (AMF) (Yuan et al. 2013; Zubek et al. 2016). However, because these experiments were conducted only on a few native species or in experimental conditions, it remains unknown whether and how these mechanisms occur at the community scale *in natura*, and how they affect the composition and functions of species-rich native communities.

In order to better understand of the mechanisms involved in *S. canadensis* invasions, we investigated how the invasion gradient (which is directly related to the time since *S. canadensis* became established in the plot) affected the entire native plant community and two main constitutive functional groups (forbs and graminoids). We identified and compiled, for most of the species present in our study area, six functional traits linked to three mechanisms suspected to be at work during *S. canadensis* invasion: competition for light, competition for nutrients and disturbance of mycorrhizal interactions. We expected the distribution of trait values in the native community to vary depending on the constraints exerted by the invader and the resistance strategies of native plants [Figure 1].

To test these hypotheses, we used a two steps framework: First, we analyzed the overall impact of *S. canadensis* on the taxonomic and functional diversity of the native communities. Next, we investigated the mechanisms that might lead to these impacts by jointly analyzing the response of the five traits (in terms of CWM and CWV) to *S. canadensis* density with structural equation models (SEM) [Figure 2].

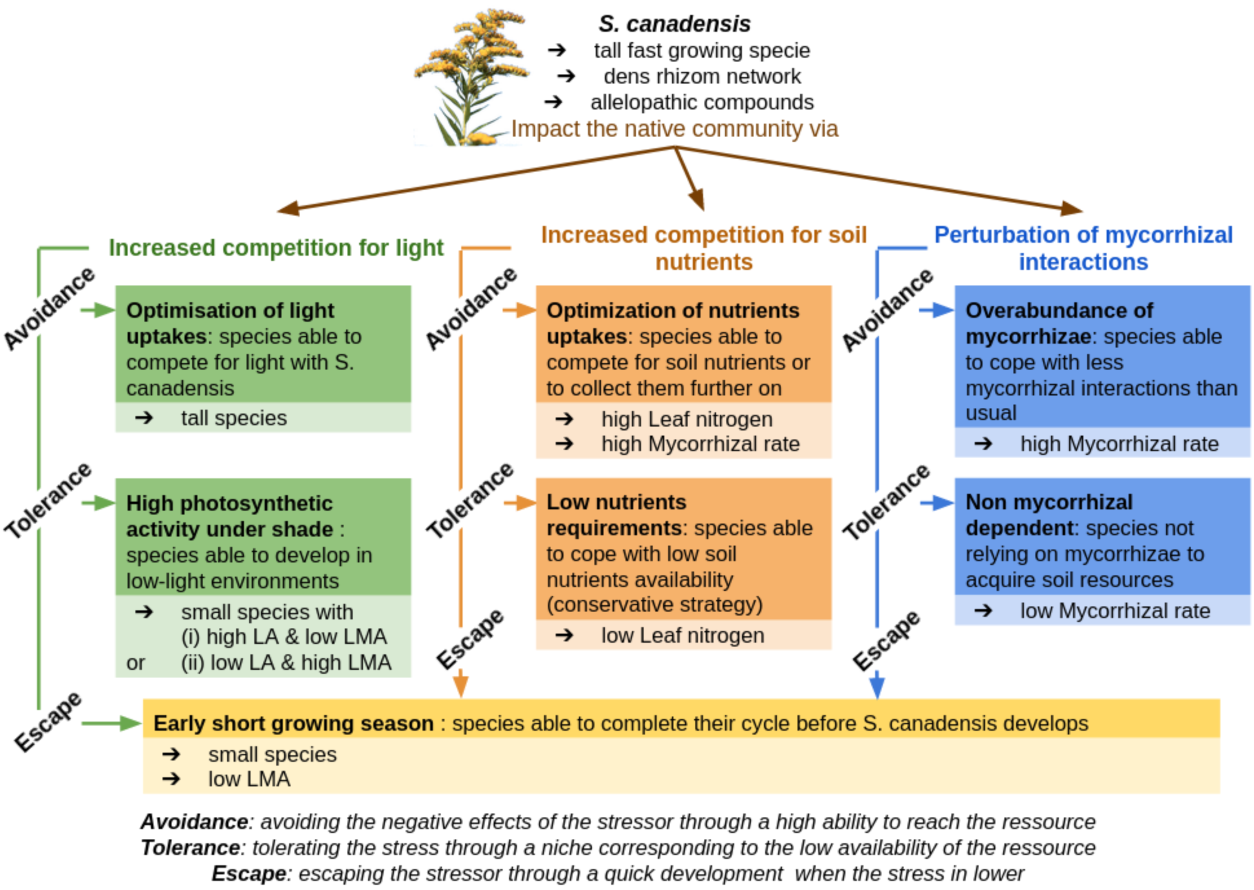


Figure 1: Three ecological strategies allowing native species to persist under S. canadensis invasion. We consider three major constraints entailed by the presence of S. canadensis: competition for light, competition for nutrients, and perturbation of mycorrhizal interactions, and three possible resistance strategies: avoidance, tolerance, and escape strategies (definition in the bottom panel). For each constraint and each resistance strategy, we present our working hypotheses regarding the expected functional characteristics of native species. LA: leaf area. LMA: leaf mass per area.

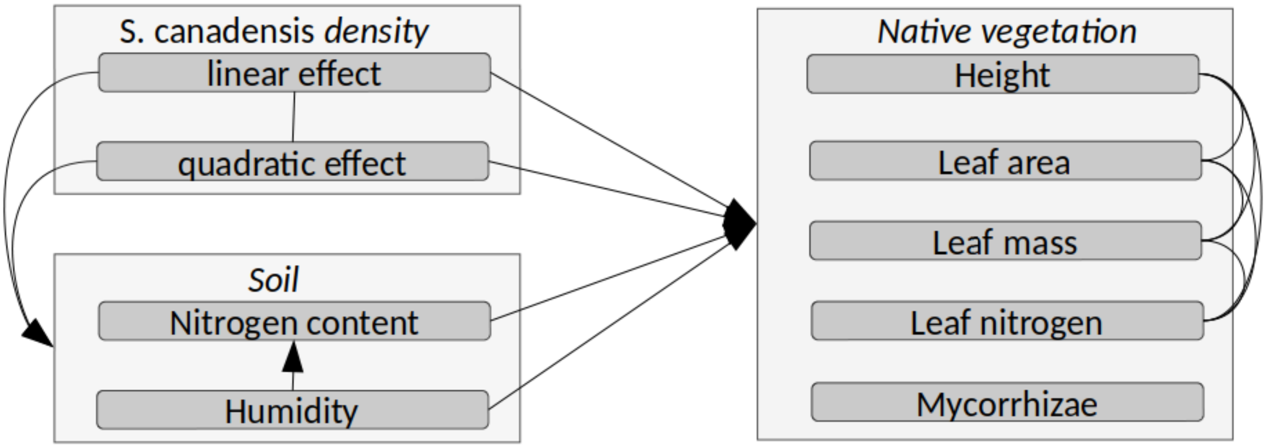


Figure 2: A priori structure of the structural equation models. Arrows represent directed links (causal relationships), and lines connecting traits represent undirected links (residual correlations) included in the model to account for allometric constraints and the relationship between the linear and quadratic component of S. canadensis density. When an arrow points from a variable to a compartment, the variable is an explanatory variable for all variables in the compartment.

Materials Methods

1. Study system

Solidago canadensis (L., 1753) is a rhizomatous Asteraceae from North America, introduced to Europe as an ornamental species during the 18th century and now naturalized in many countries (Pyšek et al. 2009). Since then, it has become one of the most invasive plants in European and Asian wetlands, where it forms dense, monospecific stands (Weber 1998; de Groot et al. 2007; Moroń et al. 2018). *S. canadensis* affects native plant communities, not only through direct competition for light, space, and soil resources (Werner et al. 1980; Gordon 1998), but also indirectly through modification of biogeochemical cycles and soil characteristics such as water and nutrient availability (Vilà et al. 2011). In addition, *S. canadensis* produces allelopathic compounds impacting associations with mycorrhizal fungi (Zhang et al. 2007).

We selected six wet meadows with similar vegetation types (belonging to EUNIS categories E3.41; E3.51 and D4.13, depending on the meadow) and management (late mowing with organic matter removal), in two protected areas of the French Alps. All meadows are geographically and environmentally close to each other so they can be considered as pseudo-replicates, and they show a broad gradient of *S. canadensis* density (0 to 170 stems of *S. canadensis* per m², representing 0 to 99 % vegetation cover). In each meadow, we selected four 100 m² plots representative of the *S. canadensis* density gradient, except for two meadows where we could only place two plots due to spatial constraints (see map and plots individual density in Supporting information).

The advantage of this study system is that the density gradient of *S. canadensis* likely represents the time since its establishment – not the invasibility of the different areas. This is because the meadows were homogeneous in native species prior to invasion and the distribution of *S. canadensis* independent of local edaphic conditions (no significant effect of humidity, nitrogen content, pH, organic matter or granulometry in a mixed-effect model, results not shown). If *S.*

canadensis has established in meadows regardless of the resistance of native vegetation and soil conditions, then its density can be assumed to reflect the time since establishment, or invasion stage. The corollary to this assumption is that the variations in native vegetation along *S. canadensis* gradients are indeed the result from invasion-induced constraints (e.g., increased competition for light).

All fieldwork was conducted during two consecutive weeks of Jun 2019. During this year, the mean annual temperature of the sites was 11.7 °C (mean of the coldest month: 1.4 °C; mean of the warmest month: 22.3 °C), and the mean annual precipitation was 1157.9 mm (Climatologie de l'année 2019 à Annecy-Meythet - Infoclimat).

2. Sampling design

2.1. Soil characteristics

In each plot, we extracted and pooled 15 soil cores (using a 15 cm deep, 5 cm wide auger). We then measured five soil characteristics: pH, humidity at the date of sampling (hereafter humidity), organic matter, total C, and total N (see details in Supporting information). pH did not vary significantly between plots (7.19 to 7.69), and organic matter content as well as total C were strongly correlated with humidity (Pearson's r of 0.87 and 0.89). Therefore, we considered only soil humidity and N content in subsequent analyses. All soil samples were extracted within two days to be representative of the differences between plots during the vegetative period, even if they do not inform on winter water regime.

2.2. Vegetation surveys

We characterized the plant communities using a point-intercept sampling method (Jonasson 1988) in four 1 m² quadrats per plot, hence for a total of 80 quadrats. All quadrats were visited within two weeks, starting with the meadows where the vegetation development seemed most advanced. In each quadrat, we placed 16 vertical pins on a grid and recorded the number of contacts of each species (multiple contacts per species per pin being recorded). Because the meadows are mown annually at the end of the summer, the total number of contacts (excluding *S. canadensis* contacts) represents both the yearly biomass production, and the abundance of the native plant community during the year (Bråthen and Hagberg 2004). For *S. canadensis*, the number of contacts is directly linked to the number of stems, and we used this metric to quantify its density.

We classified each species as either graminoid (Poaceae, Juncaceae and Cyperaceae) or forb, because these functional groups have different developmental and foraging strategies and may thus respond differently to invasion (Münkemüller et al. 2014). For example, we expected forbs to be more affected than graminoids by allelopathic perturbation of AMF interactions, as they are generally more dependent on AMF for nutrient acquisition (Wilson and Hartnett 1998). Some N-fixing species were also present, but too scarce to be taken into account in the analyses as a group in itself.

3. Data analysis

3.1. Compiling native plant traits

For each plant taxon, we reported vegetative height (Height (cm)), Leaf area (LA (cm²)), leaf mass per area (LMA (g/cm)), leaf nitrogen per leaf area (LNA (mmol/m²)), end of the flowering season (flowering date (day)) and rate of root colonization by arbuscular mycorrhizal fungi (AMF rate (%)). All traits were available for at least 75 % of the biomass production of each functional group in each quadrat (Pakeman and Quested 2007), and were less than 30 % correlated with each other (except graminoid Height and LA, see Supporting information). The five traits were extracted from freely available databases such as TRY (Kattge et al. 2020), LEDA (Knevel et al. 2003), BiolFlor (Kühn et al. 2004), and Ecoflora (Fitter and Peat 1994). Since plant functional traits can be plastic, using mean trait values from databases prevents us from identifying resistance strategies operating via trait variation within species (e.g., individuals growing taller when *S. canadensis* present). Nevertheless, given the high interspecific trait variability in our study system (Figure S2), we could still detect filtering processes operating at the species level (e.g., decreasing abundance of short species with *S. canadensis* density). We propose that native species can resist the constraints induced by *S. canadensis* invasion via three main resistance strategies: avoid, tolerate, escape, and that each strategy should leave a distinct functional trait signal (Figure 1). For example, increased competition for light and soil nutrients due to *S. canadensis* could select species with an avoidance strategy, i.e., species highly competitive for these resources (tall species and species with high LNA), and/or species with a tolerance strategy, i.e., species with low requirements for these resources (low shade-tolerant species, species with low LNA adapted to poor soils). Allelopathic compounds released by *S. canadensis* could select for species having strong interactions with AMF (high infection rate), as these species are able to compete with *S. canadensis* for AMF interactions, and could suffer minimal damage if some are lost (avoidance strategy). Alternatively, the allelopathic compounds could select species that do not rely on interactions with AMF (tolerance strategy). Finally, *S. canadensis* invasion could select for species able to escape these constraints by completing their cycle before it starts developing (small species flowering early).

3.2. Taxonomic and functional diversity

For each quadrat, we calculated two taxonomic and three functional diversity indices based on the traits presented above: (i) taxonomic richness (Richness), (ii) taxonomic equitability of abundances (exponential of the Shannon index, hereafter called Evenness, Hill 1973; Jost et al. 2010), (iii) functional richness (FRich), (iv) functional evenness (FEve), (vi) functional divergence (FDiv) (Mason et al. 2005). FRich, FEve, and FDiv indicate, respectively, the size of the community’s functional space, the equitability of biomass repartition, and the eccentricity of biomass repartition in that space (at the center or periphery of the space). We calculated these indices for the entire plant community, and separately for forbs and graminoids. Because invasion by *S. canadensis* induces new constraints - due to its high competitiveness and allelopathic compounds production - we expected it to lead to a decrease in biomass production, taxonomic diversity, functional richness, and functional evenness, but also to an increase in functional divergence (selection of species resisting to different constraints and/or with different resistance strategies).

We also calculated the community weighted mean (CWM) and community weighted variance (CWV) of the five functional traits selected for forbs and graminoids separately, as we expected the two functional groups to respond differently to *S. canadensis* density. We hypothesized that these CWM and CWV would vary according to the resistance strategy of the focal functional group (Figure 1).

3.3. Statistical analyses

All variables were standardized prior to analyses to avoid size effects and to make it possible to compare the estimated parameters within and between analyses.

First, we assessed the impact of *S. canadensis* density on native plant communities in terms of biomass production and diversity (Richness, Evenness, FRich, FEve, FDiv). We designed mixed-effect linear models to analyze the response of each of these variables to *S. canadensis* density (with both linear and quadratic effects), soil humidity and nitrogen content. We included the meadow identity (hereafter called meadow ID) as a random effect to account for differences among sites. We built the models considering the entire native communities, as well as for native forb and graminoid assemblages separately. We assessed model performance using marginal and conditional R^2 goodness-of-fit.

Second, we used structural equation models (SEMs) to disentangle the direct and indirect mechanisms (through plant-soil interactions) through which *S. canadensis* impacts native forbs and graminoids. We built four SEMs, corresponding to two summary statistics of trait distribution (CWM and CWV) applied to the two native species functional groups (forbs and graminoids). In each SEM, *S. canadensis* density (linear and quadratic effects) could directly affect soil characteristics and plant traits distribution. Soil characteristics could directly affect each trait, and soil humidity could directly affect soil nitrogen content. To account for allometric constraints in plants (Weiner 2004; Lefcheck 2016), correlations between plant traits were integrated into the SEMs (except for Mycorrhiza). We used the hypothesized linkages between plant-soil compartments to design the structure of our initial SEMs [Figure 2], which we simplified and improved following a three-step procedure. We (i) ran our initial model, and improved it by (ii) iteratively adding links when independence claims were not supported by the test of directed separation (p-value < 0.05), and (iii) iteratively removing links that were not significant (p-value > 0.05) (Grace et al. 2015). To confirm that *S. canadensis* impacted soil characteristics and not the reverse, we constructed another set of models where we reversed the direction of the links between *S. canadensis* and the soil compartment. The BIC, AIC, and Fisher’s C-value confirmed our hypothesis for all models.

All statistical analyses were conducted in R v.3.6.3 (R Core Team 2020) with the packages TR8 (Bocci 2020), lme4 (Bates et al. 2021), lmerTest (Kuznetsova et al. 2020), MuMIn (Bartoń 2020) and piecewiseSEM (Lefcheck 2016).

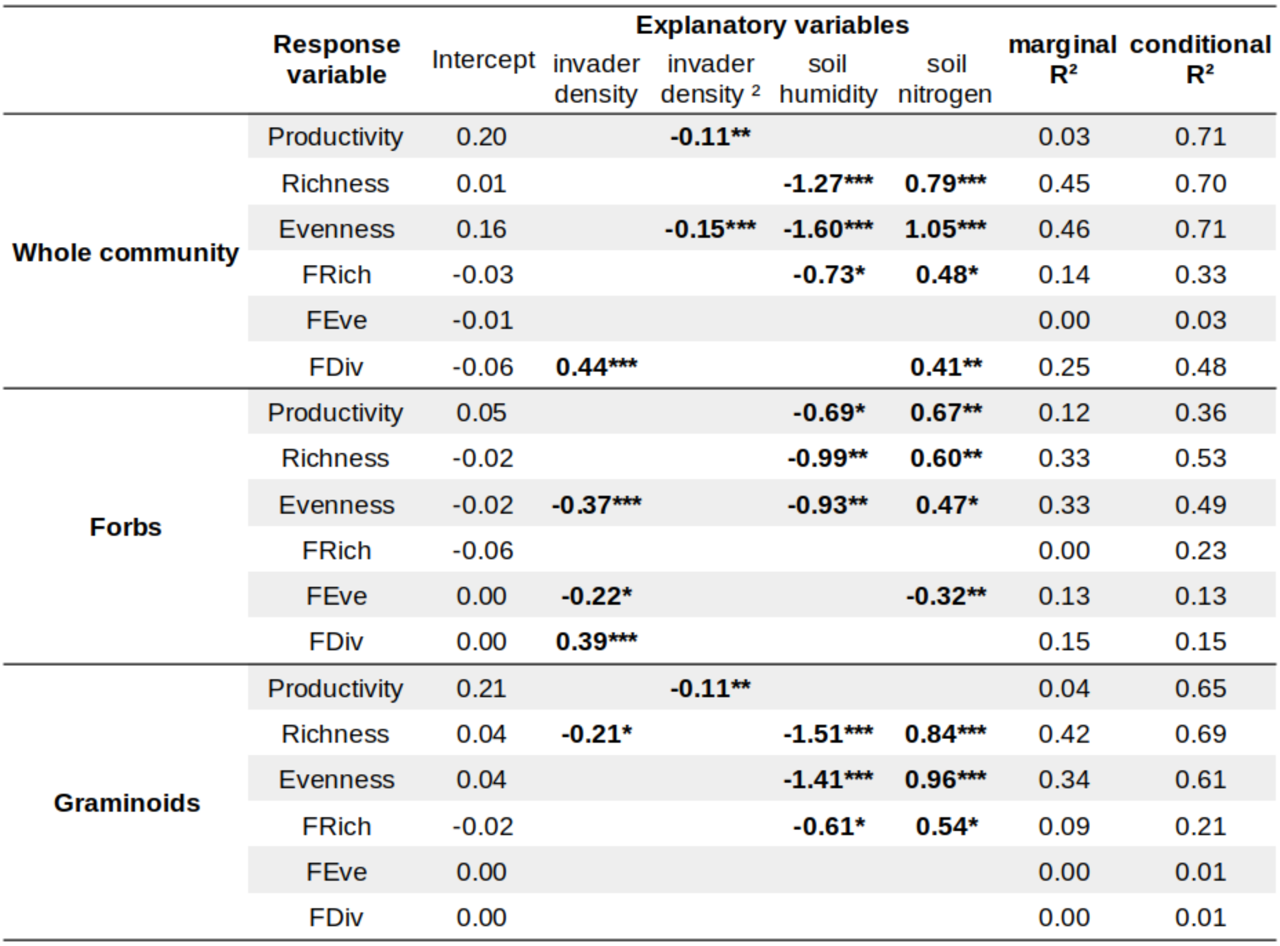
Results

We recorded a total of 102 plant species and 24 taxa identified to a higher taxonomic level (Supporting information), with an average of 14 species and 129 contacts per quadrat. 41 % of contacts represented forbs species and 59 % represented graminoid species.

1. Impacts of *S. canadensis* native plant biomass production and diversity

The density of *Solidago canadensis* had distinct effects on graminoids and forbs. Increase in invader density was correlated to a decrease in graminoid Richness (linear effect) and Biomass production (quadratic, unimodal effect), whereas for forbs it was associated to a decrease in the taxonomic and functional evenness, and to an increase in the functional divergence (linear effects). Indices calculated on the whole community varied in the same direction, but were significant only for Biomass production, Evenness, and FDiv. We observed a negative effect of soil humidity and a positive effect of soil nitrogen on: Richness (community and functional group levels), Evenness (community and functional group levels), FRich (community and graminoids), and Biomass production (forbs). In addition, the random effect on meadow ID explained a large part of the observed variations (up to 68 %). The coefficients and their p-values as well as the marginal and conditional R^2 of all mixed-effect models are presented in Table 1, and the response curves of models with a significant effect of *S. canadensis* are presented in Supplementary information.

Table 1: Parameter estimates of the mixed effect models of the impact of S. canadensis (linear and quadratic effects) and soil resources on the diversity indices for the whole community, as well as for forbs and of graminoids taken apart. Values in bold indicate significant effects (p-value < 0.05; ** p-value < 0.01; *** p-value < 0.001). Model performance is reported with both marginal* R^2 *(proportion of variance explained by fixed factors) and conditional* R^2 *(proportion of variance explained by fixed and random factors).*



	Response variable	Intercept	**Explanatory variables**				**marginal R²**	**conditional R²**
			invader density	invader density ²	soil humidity	soil nitrogen		
Whole community	Productivity	0.20		**-0.11****			0.03	0.71
	Richness	0.01			**-1.27*****	**0.79*****	0.45	0.70
	Evenness	0.16		**-0.15*****	**-1.60*****	**1.05*****	0.46	0.71
	FRich	-0.03			**-0.73***	**0.48***	0.14	0.33
	FEve	-0.01					0.00	0.03
	FDiv	-0.06	**0.44*****			**0.41****	0.25	0.48
Forbs	Productivity	0.05			**-0.69***	**0.67****	0.12	0.36
	Richness	-0.02			**-0.99****	**0.60****	0.33	0.53
	Evenness	-0.02	**-0.37*****		**-0.93****	**0.47***	0.33	0.49
	FRich	-0.06					0.00	0.23
	FEve	0.00	**-0.22***			**-0.32****	0.13	0.13
	FDiv	0.00	**0.39*****				0.15	0.15
Graminoids	Productivity	0.21		**-0.11****			0.04	0.65
	Richness	0.04	**-0.21***		**-1.51*****	**0.84*****	0.42	0.69
	Evenness	0.04			**-1.41*****	**0.96*****	0.34	0.61
	FRich	-0.02			**-0.61***	**0.54***	0.09	0.21
	FEve	0.00					0.00	0.01
	FDiv	0.00					0.00	0.01

2. *S. canadensis* impacts on native trait distribution

The four structural equation models (SEMs) had statistically robust structure (Fisher's C p-value > 0.45). They revealed no significant relationship between *S. canadensis* density and soil variables (humidity and N content), and humidity had a positive effect on soil nitrogen content.

The effects of soil characteristics and *S. canadensis* density on native plant characteristics (in terms of trait mean or variance) varied between forbs and graminoids (Figures 3, 4). It can be noted that all significant *S. canadensis* density effects were linear (no hump-shaped relationship detected).

Within the native forbs, *S. canadensis* directly selected for tall species, species with high LNA and species with high AMF infection rates. It also selected indirectly for species with high LA, high LMA and early end of flowering (via allometric constraints with plant heights, LNA and AMF infection rates) (Figure 3.a). We found no impact of *S. canadensis* on the variance of forb traits

(Figure 3.b). Regarding the effects of soil characteristics, we found that N-richer soils favored smaller species, species with low AMF infection rates and species with an early end of flowering. Soil humidity favored tall species, species with low LMA and species with intermediate LNA, while counter-selecting species with intermediate AMF infection rate [Figure 3].

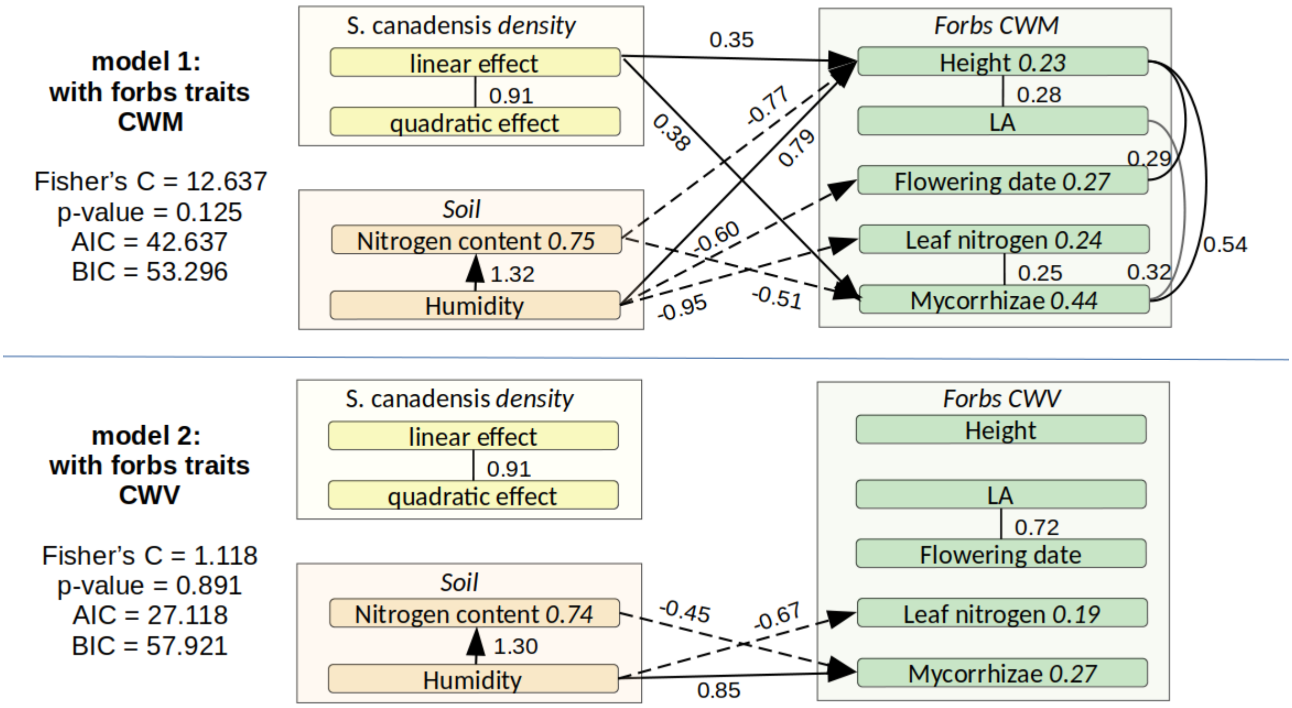


Figure 3: Structural equation models representing the impact of S. canadensis density on trait means (CWM, model 1) and variances (CWV, model 2) of forb species. Black solid and dashed arrows represent significant positive and negative directed impacts (p-value < 0.05), respectively. Black lines represent significant positive undirected relationships (p-value < 0.05). The coefficients associated with each significant link are indicated beside the corresponding arrows and lines, and the values beside the response variables are their associated marginal R². The structure of the initial model (i.e., before variable and link selection) is shown on Figure 2. Some links were removed (when not significant) and others added (to support independence claims) to the initial models following the model building procedure described in Materials and Methods.

In the graminoid, high densities of *S. canadensis* was directly correlated to a decrease in species of medium height (positive effect on the variance of plant heights in graminoids), and/or medium LA (positive effect on CWV). Invader density was also indirectly linked to a decrease in species with an intermediate end of flowering, and extreme values of mycorrhizal infection (via allometric constraints with plant heights) (Figure 4.b). We found no impact of *S. canadensis* on the mean values of graminoid traits (Figure 4.a). Regarding the effects of the soil characteristics, we found that richer soils (high N content) favored species with low LMA and AMF infection rate. Soil humidity favored tall species, species with high LMA, species with intermediate LNA and selected against species with intermediate end of flowering (Figure 4).

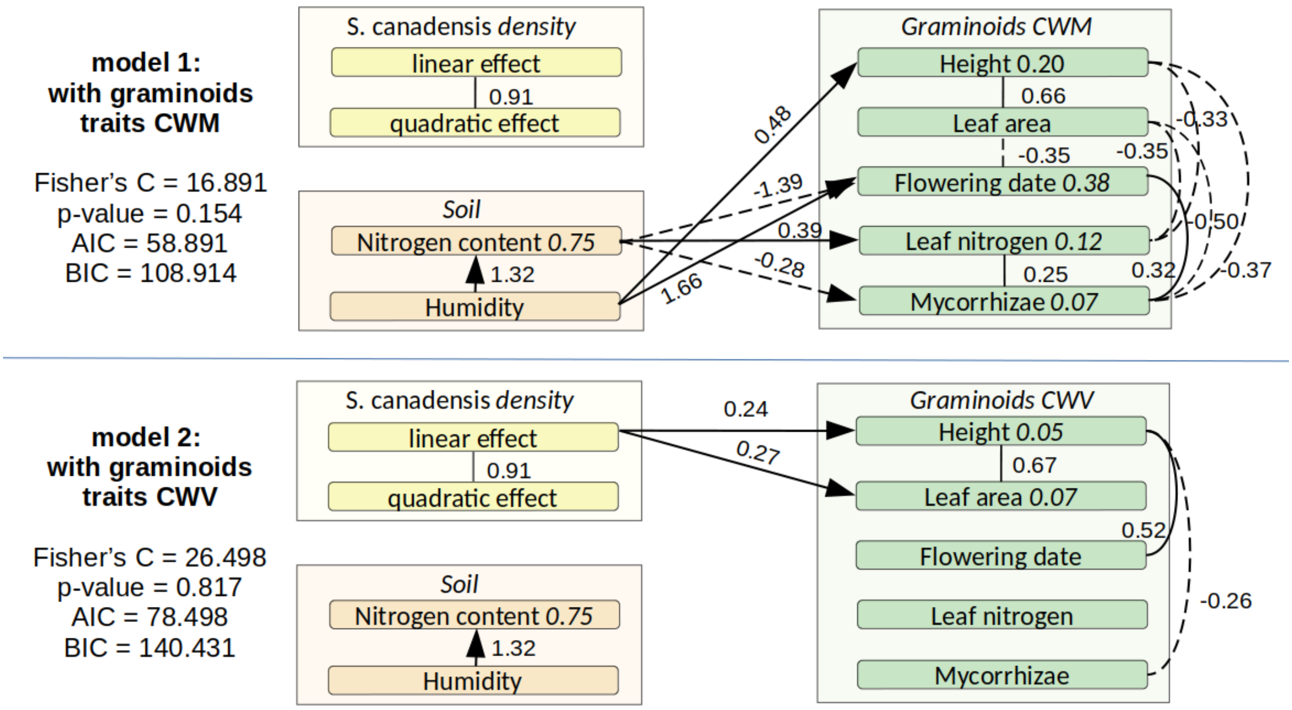


Figure 4: Structural equation models representing the impact of S. canadensis density *on trait means (CWM, model 1) and variances (CWV, model 2) of graminoid species. Black solid and dashed arrows represent significant positive and negative directed impacts (p-value < 0.05), respectively. Black lines represent significant positive undirected relationships (p-value < 0.05). The*

coefficients associated with each significant link are indicated next to the corresponding arrows and lines, and the values beside the response variables are their associated marginal R². The structure of the initial model (i.e., before variable and link selection) is shown on Figure 2. Some links were removed (when not significant) and others added (to support independence claims) to the initial models following the model building procedure described in Materials and Methods.

Discussion

We found an overall negative impact of *Solidago canadensis* on native vegetation biomass production and diversity, but the magnitude of these impacts depended on functional groups (native forbs vs. graminoids). For example, *S. canadensis* reduced the richness and biomass production of graminoids, but not those of forbs. A high density of *S. canadensis* tended to select only forb species avoiding the new constraints (competition for light, nutrients and perturbation of mycorrhizal interaction) through their high ability to reach the resources with low LMA and AMF infection rate. In contrast, it selected graminoid species that either avoid (competition for light), tolerate (competition for light), or escape (rapid early season growth) the constraints due to *S. canadensis* preemption of light. Finally, soil conditions are important determinants of native community structure and composition in the sampled wet meadows (Maltby and Barker 2009), but are independent from *S. canadensis* density. Thus, we observed no indirect effect of *S. canadensis* on native plants through changes in soil humidity or nitrogen due to the invasion. This also supports our hypothesis that *S. canadensis* randomly established within the meadows, independently of local variations in edaphic conditions and native plant communities.

1. Impacts of *S. canadensis* on native species biomass production and diversity: different responses between functional groups

Invasion by *S. canadensis* negatively impacted both forbs and graminoids in terms of biomass production, taxonomic or functional diversity, but the metrics of diversity that were affected differed between the two functional groups. These results support the idea that the two functional groups respond differently to abiotic and biotic constraints (Bowman et al. 1995; Freschet et al. 2018; Raevel et al. 2018) and reveal that one invader can affect different functional groups of plants via different mechanisms. Importantly, at the community level, we only detected part of the *S. canadensis* effects detected at the functional group level: loss of Biomass production, loss of Evenness and gain in FDiv. This demonstrates that differences in response to invasion between functional groups, in terms of taxonomic and functional diversity, can blur signals at the community level and lead to an underestimation of the impacts of invasions (Münkemüller et al. 2014).

For forb species, we showed that as *S. canadensis* density increased, the biomass production of forbs was less evenly distributed across species and traits (reduced taxonomic and functional evenness), and species with intermediate traits became less abundant compared to those at the periphery of the community's functional space (increased FDiv). This may create vacant niches at the center of forbs functional space that could increase the probability of other exotic species invasion (Moles et al. 2008). In contrast, for graminoid species, an increase in *S. canadensis* density entailed decreasing richness and biomass production, but we did not detect any signal on functional diversity.

2. Impacts of *S. canadensis* on native plant traits: resistance strategies differ depending on functional groups and constraints

2.1. Competition for light

Solidago canadensis is a tall species (up to 2 m), with an abundant foliage all along the stem and close stems. High densities of *S. canadensis* can thus generate a strong competition to native species requiring direct light. We detected this constraint for both forbs and graminoids: we observed taller native species at higher invader density. Tall forbs and graminoids are able to intercept light with their upper parts and are thus less affected by the shade of *S. canadensis*, which corresponds to an avoidance strategy. Interestingly, in parallel, short graminoids were also increasingly prevalent along the invasion gradient. This could be due to their naturally good capacity to tolerate shade, since short species are often under the canopy of native species as well, corresponding to a tolerance strategy. In addition, short graminoids could benefit from the fact that they also tend to flower earlier than tall species (due to allometric constraints; Supplementary materials) and may thus be able to complete their cycle before *S. canadensis* outgrows them (stem elongation starting in late April and reaching final size late July), corresponding to an escape strategy. *S. canadensis* also indirectly selects forb species with an early end of flowering that might be able to escape competition for light, soil nutrients and mycorrhizal interactions.

2.2. Competition for soil nutrients and mycorrhizal interactions

S. canadensis is known to be a fast-growing species, building a dense network of rhizomes and small roots with a high mycorrhizal infection rate that allows efficient nutrient uptake (Werner et al. 1980; Yang et al. 2014; Dong et al. 2021). It is also known to produce allelopathic compounds in the soil that inhibit the growth of other plants and their interactions with mycorrhizae (Zhang et al. 2007; Zubek et al. 2016). We detected this constraint only for forbs: *S. canadensis* selected forbs with high AMF infection rate (direct effect) and high leaf nitrogen content per leaf area (LNA, indirect effect via AMF infection rate). These species are able to (i) avoid competition for local soil nutrients by reaching resources outside the rhizosphere of *S. canadensis* (high LNA, Cunningham et al. 1999), and possibly (ii) avoid part of the allelopathic perturbations of AMF interactions as they easily form interactions and may lose part of them without being too much affected. The fact that graminoids were not affected by the increased competition for nutrients and the perturbation of mycorrhizal interactions may be due to the fact that they have nutrients uptake strategy is different from that of forbs (different root systems) and they already have low mycorrhizal interactions (Figure S2).

3. Conclusions on the different strategies

Overall, our results indicate that, in our study system, the impacts of *S. canadensis* on graminoids are primarily due to competition for light, while forbs are also affected by competition for soil nutrients and alteration of mycorrhizal interactions. Furthermore, the positive impact of *S. canadensis* density on forbs functional divergence suggests that the selection for height and AMF interactions does not apply to the same species: different species may be selected for their ability to resist to different constraints. *S. canadensis* being a forb, it has a below- and above-ground structure more similar to native forbs than to native graminoids. Because competition arises when different species have similar ways to access the same resource, *S. canadensis* compete more with native forbs and this may explain why we found evidence of three different constraints of invasion on forbs but just of one of them on graminoids. Interestingly, we found no indirect effect of *S. canadensis* on native vegetation through the soil compartment, as *S. canadensis* did not affect soil humidity and nitrogen content, supporting the results found by Scharfy et al. (2010) on similar wet meadows (but Zhang et al. (2009) found effects of *S. canadensis* on soil properties under a subtropical monsoon climate).

4. Limits and Perspectives

In invasion studies, it is often difficult to disentangle the causes from the consequences of invasion (Gallien and Carboni 2017): do the traits of native species in invaded communities reveal the cause of their invasion (i.e., the driver of their “invasibility”) or their response to the invader (i.e., a sign of the filtering imposed by the invader)? To avoid this pitfall and isolate only native species responses to invasion by *S. canadensis*, we selected the meadows of this study to be as homogeneous as possible in terms of management history, edaphic conditions, and vegetation. In addition, each meadow contained a gradient of invader density independent from any gradient of edaphic conditions. Therefore, we can assume that prior to the invasion, there was no difference within the prospected meadows - in terms of community taxonomic and functional structures - that would explain the current repartition of *S. canadensis*. In other words, the differences we currently observe along this gradient are likely the result of the effects of the invader, and the density of *S. canadensi*s a function of its stage of invasion (not of community invasibility). It should be noted that we probably underestimated or missed some of these differences because we were not able to detect plastic responses. Studying trait responses at the species level would be the next step to improve our understanding of invasion impacts.

Another difficulty when studying the impact of invasions on native vegetation is its dynamic nature. During invasion, the density of the invader increases over time, but native vegetation responses may take years to appear (Rusterholz et al. 2017). At a given density of the invader, some native species may show (i) colonization credit (i.e., natives that were locally excluded by dominant native species before invasion can now colonize sites where S. canadensis has replaced these dominant natives), or (ii) extinction debt (i.e., populations that are currently present in the patch, but will disappear because their population growth rate is less than one) (Jackson and Sax 2010; Bagaria et al. 2015; Rumpf et al. 2019). In this study, *S. canadensis* patches were small enough (<300 m²) for the native vegetation to recolonize the patch through a high propagule pressure, potentially leading to lower colonization credits and higher extinction debts compared to large invaded areas. Extinction debt was also promoted by the fact that most species in our study site are perennials: individuals can survive for years even if propagules fail to establish. These dynamic effects are generally difficult to eliminate, but the fact that colonization credits are limited, while extinction debts are likely present, tends to make our results more conservative about the magnitude of *S. canadensis* effects (i.e., we might have missed some mechanisms that are not yet detectable due to the extinction debt).

Finally, in this study, we focused on mechanisms and traits linked to the vegetative development of native plant species. However, *S. canadensis* may impact native species through other mechanisms. For example, it could reduce native plant reproduction success through (i) competition for pollinators, (ii) pollen competition, or (iii) allelopathic compounds limiting natives germination and growth (Abhilasha et al. 2008; Yuan et al. 2013; Sun et al. 2013). In particular, *S. canadensis* is known to produce abundant, high-quality pollen and nectar at the end of the flowering season, and thus to act as an important resource for honeybees and some wild pollinators (Stefanic et al. 2003; Fenesi, Vágási, et al. 2015; Grange et al. 2021). Dense patches of *S. canadensis* could therefore disturb native pollination networks and fruit sets (i) positively by attracting more generalist pollinators from the landscape pool (concentration effect; Ghazoul 2006), and/or (ii) negatively by increasing inter-specific competition for pollinators (dilution effect; Campbell and Hanula 2007; Morales and Traveset 2009). Further investigation of the *S. canadensis* influences on native plant-pollinator interactions seems thus as an important next step toward a more comprehensive understanding of invasion impacts through cascading effects.

Conclusion

Our study showed that the invader *S. canadensis* has a complex effect on native vegetation. Its impacts vary between and within functional groups: forbs and graminoids responded to different constraints and we detected different strategies for resisting the same constraint within graminoids. Our results show that those native forbs that survive invasion use an avoidance strategy to respond to increased competition for light, soil nutrients and AMF interactions (i.e. they avoid the stress by having good abilities to reach the resources), whereas graminoids use all types of resistance strategies (avoidance, tolerance and escape) to respond to increased competition for light. Considering traits linked to different constraints and strategies for different functional groups seems thus essential to understand the complexity of the native vegetation response to invasion. Applying such an approach in future studies may ultimately help us understand why the same invasive species can have opposing impacts on native communities of different compositions.

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Statements Declarations

1. Data availability statement

The data used in the analyses are available in the supplementary material. All raw and derived data supporting the findings of this study are available from the corresponding author Marie Charlotte Grange on request.

2. Funding statement

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3. Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

4. Author Contributions

Marie Charlotte Grange, Laure Gallien and François Munoz contributed to the conception and design of the study. Material preparation and data collection were performed by all authors. The database was created by Julien Renaud. Analyses were performed by Marie Charlotte Grange. The first draft of the manuscript was written by Marie Grange and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.