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

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18 **Abstract**

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

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

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

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

40

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

43

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47 their insightful comments that helped us to significantly improve the manuscript.

48

## Introduction

49

50 Invasive plants are known to alter native plant communities and their functions in an  
51 ecosystem through a variety of mechanisms (Vilà et al. 2011; Pyšek et al. 2012; Castro-Díez et al.  
52 2016). They are often strong competitors for resources (Gioria and Osborne 2014), can affect  
53 biogeochemical cycles (Zhang et al. 2019), arthropod and mycorrhizal communities (Litt et al.  
54 2014; Yuan et al. 2014; Davis et al. 2018), and the interactions of these groups with the native  
55 vegetation (Albrecht et al. 2014). Through these mechanisms, they may jeopardize the functioning  
56 of the entire ecosystem (Gordon 1998; Vilà et al. 2011).

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

65 Native plant species can employ three possible strategies to resist invasion: avoidance,  
66 tolerance, and escape (Figure 1) (Levitt 2015; Yıldırım and Kaya 2017). Little is known about the  
67 relative importance of the three strategies to allow persistence in the face of invasion, although  
68 these strategies are well known regarding other stresses such as drought (Bodner et al. 2015; Volaire  
69 2018). The *avoidance strategy* refers to native species with sufficiently good abilities to acquire the  
70 resources they need regardless of the invader presence (e.g., being tall if the constraint is on light  
71 interception, Craine and Dybzinski 2013). The *tolerance strategy* refers to species requiring limited  
72 amounts of resources to complete their life cycle (e.g., shade tolerant species, Valladares and

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

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

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

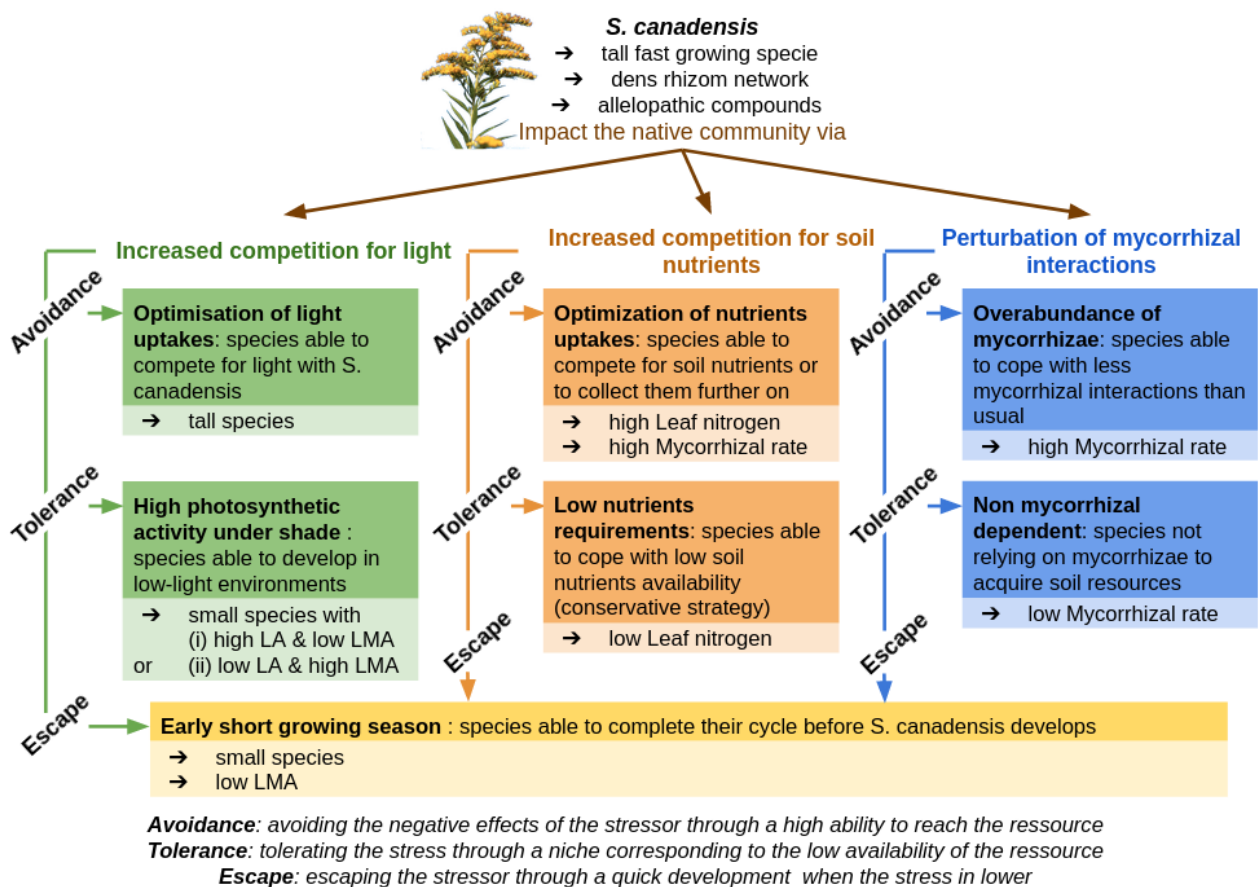
107       In this study, we characterized the impacts of *Solidago canadensis* (L., 1753) on native plant  
108 communities and the mechanisms underlying these impacts in recently colonized (less than 50 years  
109 old) French wet meadows encompassing a broad invasion gradient. *S. canadensis* one of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

118       In order to better understand of the mechanisms involved in *S. canadensis* invasions, we  
119 investigated how the invasion gradient (which is directly related to the time since *S. canadensis*  
120 became established in the plot) affected the entire native plant community and two main  
121 constitutive functional groups (forbs and graminoids). We identified and compiled, for most of the

122 species present in our study area, six functional traits linked to three mechanisms suspected to be at  
 123 work during *S. canadensis* invasion: competition for light, competition for nutrients and disturbance  
 124 of mycorrhizal interactions. We expected the distribution of trait values in the native community to  
 125 vary depending on the constraints exerted by the invader and the resistance strategies of native  
 126 plants [Figure 1].

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

132

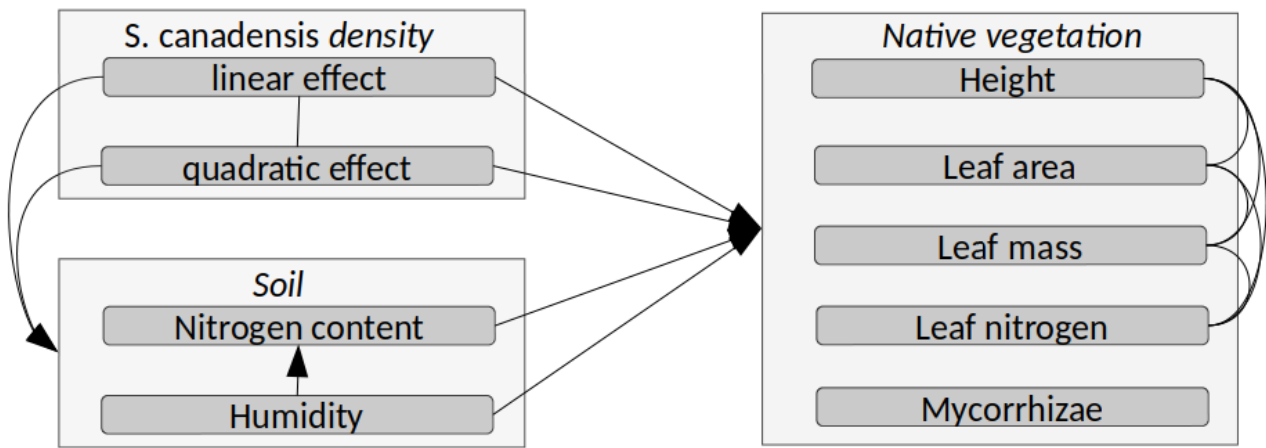


133



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

141



142

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

148

## Materials Methods

### 1. Study system

149  
150  
151 *Solidago canadensis* (L., 1753) is a rhizomatous Asteraceae from North America, introduced  
152 to Europe as an ornamental species during the 18th century and now naturalized in many countries  
153 (Pyšek et al. 2009). Since then, it has become one of the most invasive plants in European and  
154 Asian wetlands, where it forms dense, monospecific stands (Weber 1998; de Groot et al. 2007;  
155 Moroń et al. 2018). *S. canadensis* affects native plant communities, not only through direct  
156 competition for light, space, and soil resources (Werner et al. 1980; Gordon 1998), but also  
157 indirectly through modification of biogeochemical cycles and soil characteristics such as water and  
158 nutrient availability (Vilà et al. 2011). In addition, *S. canadensis* produces allelopathic compounds  
159 impacting associations with mycorrhizal fungi (Zhang et al. 2007).

160 We selected six wet meadows with similar vegetation types (belonging to EUNIS categories  
161 E3.41; E3.51 and D4.13, depending on the meadow) and management (late mowing with organic  
162 matter removal), in two protected areas of the French Alps. All meadows are geographically and  
163 environmentally close to each other so they can be considered as pseudo-replicates, and they show a  
164 broad gradient of *S. canadensis* density (0 to 170 stems of *S. canadensis* per m<sup>2</sup>, representing 0 to  
165 99 % vegetation cover). In each meadow, we selected four 100 m<sup>2</sup> plots representative of the *S.*  
166 *canadensis* density gradient, except for two meadows where we could only place two plots due to  
167 spatial constraints (see map and plots individual density in Supporting information).

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

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

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

## 182 **2. Sampling design**

### 183 **2.1. Soil characteristics**

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

### 192 **2.2. Vegetation surveys**

193 We characterized the plant communities using a point-intercept sampling method (Jonasson  
194 1988) in four 1 m<sup>2</sup> quadrats per plot, hence for a total of 80 quadrats. All quadrats were visited  
195 within two weeks, starting with the meadows where the vegetation development seemed most  
196 advanced. In each quadrat, we placed 16 vertical pins on a grid and recorded the number of contacts

197 of each species (multiple contacts per species per pin being recorded). Because the meadows are  
198 mown annually at the end of the summer, the total number of contacts (excluding *S. canadensis*  
199 contacts) represents both the yearly biomass production, and the abundance of the native plant  
200 community during the year (Bråthen and Hagberg 2004). For *S. canadensis*, the number of contacts  
201 is directly linked to the number of stems, and we used this metric to quantify its density.

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

### 209 **3. Data analysis**

#### 210 **3.1. Compiling native plant traits**

211 For each plant taxon, we reported vegetative height (Height (cm)), Leaf area (LA (cm<sup>2</sup>)), leaf  
212 mass per area (LMA (g/cm)), leaf nitrogen per leaf area (LNA (mmol/m<sup>2</sup>)), end of the flowering  
213 season (flowering date (day)) and rate of root colonization by arbuscular mycorrhizal fungi (AMF  
214 rate (%)). All traits were available for at least 75 % of the biomass production of each functional  
215 group in each quadrat (Pakeman and Quested 2007), and were less than 30 % correlated with each  
216 other (except graminoid Height and LA, see Supporting information). The five traits were extracted  
217 from freely available databases such as TRY (Kattge et al. 2020), LEDA (Knevel et al. 2003),  
218 BiolFlor (Kühn et al. 2004), and Ecoflora (Fitter and Peat 1994). Since plant functional traits can be  
219 plastic, using mean trait values from databases prevents us from identifying resistance strategies  
220 operating via trait variation within species (e.g., individuals growing taller when *S. canadensis*

221 present). Nevertheless, given the high interspecific trait variability in our study system (Figure S2),  
222 we could still detect filtering processes operating at the species level (e.g., decreasing abundance of  
223 short species with *S. canadensis* density). We propose that native species can resist the constraints  
224 induced by *S. canadensis* invasion via three main resistance strategies: avoid, tolerate, escape, and  
225 that each strategy should leave a distinct functional trait signal (Figure 1). For example, increased  
226 competition for light and soil nutrients due to *S. canadensis* could select species with an avoidance  
227 strategy, i.e., species highly competitive for these resources (tall species and species with high  
228 LNA), and/or species with a tolerance strategy, i.e., species with low requirements for these  
229 resources (low shade-tolerant species, species with low LNA adapted to poor soils). Allelopathic  
230 compounds released by *S. canadensis* could select for species having strong interactions with AMF  
231 (high infection rate), as these species are able to compete with *S. canadensis* for AMF interactions,  
232 and could suffer minimal damage if some are lost (avoidance strategy). Alternatively, the  
233 allelopathic compounds could select species that do not rely on interactions with AMF (tolerance  
234 strategy). Finally, *S. canadensis* invasion could select for species able to escape these constraints by  
235 completing their cycle before it starts developing (small species flowering early).

### 236 **3.2. Taxonomic and functional diversity**

237 For each quadrat, we calculated two taxonomic and three functional diversity indices based on  
238 the traits presented above: (i) taxonomic richness (Richness), (ii) taxonomic equitability of  
239 abundances (exponential of the Shannon index, hereafter called Evenness, Hill 1973; Jost et al.  
240 2010), (iii) functional richness (FRich), (iv) functional evenness (FEve), (vi) functional divergence  
241 (FDiv) (Mason et al. 2005). FRich, FEve, and FDiv indicate, respectively, the size of the  
242 community's functional space, the equitability of biomass repartition, and the eccentricity of  
243 biomass repartition in that space (at the center or periphery of the space). We calculated these  
244 indices for the entire plant community, and separately for forbs and graminoids. Because invasion  
245 by *S. canadensis* induces new constraints - due to its high competitiveness and allelopathic

246 compounds production - we expected it to lead to a decrease in biomass production, taxonomic  
247 diversity, functional richness, and functional evenness, but also to an increase in functional  
248 divergence (selection of species resisting to different constraints and/or with different resistance  
249 strategies).

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

### 255 **3.3. Statistical analyses**

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

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

266 Second, we used structural equation models (SEMs) to disentangle the direct and indirect  
267 mechanisms (through plant-soil interactions) through which *S. canadensis* impacts native forbs and  
268 graminoids. We built four SEMs, corresponding to two summary statistics of trait distribution  
269 (CWM and CWV) applied to the two native species functional groups (forbs and graminoids). In

270 each SEM, *S. canadensis* density (linear and quadratic effects) could directly affect soil  
271 characteristics and plant traits distribution. Soil characteristics could directly affect each trait, and  
272 soil humidity could directly affect soil nitrogen content. To account for allometric constraints in  
273 plants (Weiner 2004; Lefcheck 2016), correlations between plant traits were integrated into the  
274 SEMs (except for Mycorrhiza). We used the hypothesized linkages between plant-soil  
275 compartments to design the structure of our initial SEMs [Figure 2], which we simplified and  
276 improved following a three-step procedure. We (i) ran our initial model, and improved it by (ii)  
277 iteratively adding links when independence claims were not supported by the test of directed  
278 separation ( $p$ -value  $< 0.05$ ), and (iii) iteratively removing links that were not significant ( $p$ -value  $>$   
279  $0.05$ ) (Grace et al. 2015). To confirm that *S. canadensis* impacted soil characteristics and not the  
280 reverse, we constructed another set of models where we reversed the direction of the links between  
281 *S. canadensis* and the soil compartment. The BIC, AIC, and Fisher's C-value confirmed our  
282 hypothesis for all models.

283 All statistical analyses were conducted in R v.3.6.3 (R Core Team 2020) with the packages  
284 TR8 (Bocci 2020), lme4 (Bates et al. 2021), lmerTest (Kuznetsova et al. 2020), MuMIn (Bartoń  
285 2020) and piecewiseSEM (Lefcheck 2016).

## 286 **Results**

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

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

291 The density of *Solidago canadensis* had distinct effects on graminoids and forbs. Increase in  
292 invader density was correlated to a decrease in graminoid Richness (linear effect) and Biomass  
293 production (quadratic, unimodal effect), whereas for forbs it was associated to a decrease in the

294 taxonomic and functional evenness, and to an increase in the functional divergence (linear effects).  
295 Indices calculated on the whole community varied in the same direction, but were significant only  
296 for Biomass production, Evenness, and FDiv. We observed a negative effect of soil humidity and a  
297 positive effect of soil nitrogen on: Richness (community and functional group levels), Evenness  
298 (community and functional group levels), FRich (community and graminoids), and Biomass  
299 production (forbs). In addition, the random effect on meadow ID explained a large part of the  
300 observed variations (up to 68 %). The coefficients and their p-values as well as the marginal and  
301 conditional  $R^2$  of all mixed-effect models are presented in Table 1, and the response curves of  
302 models with a significant effect of *S. canadensis* are presented in Supplementary information.

303 *Table 1: Parameter estimates of the mixed effect models of the impact of S. canadensis (linear*  
304 *and quadratic effects) and soil resources on the diversity indices for the whole community, as well*  
305 *as for forbs and of graminoids taken apart. Values in bold indicate significant effects (\* p-value <*  
306 *0.05; \*\* p-value < 0.01; \*\*\* p-value < 0.001). Model performance is reported with both marginal*  
307  *$R^2$  (proportion of variance explained by fixed factors) and conditional  $R^2$  (proportion of variance*  
308 *explained by fixed and random factors).*



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

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

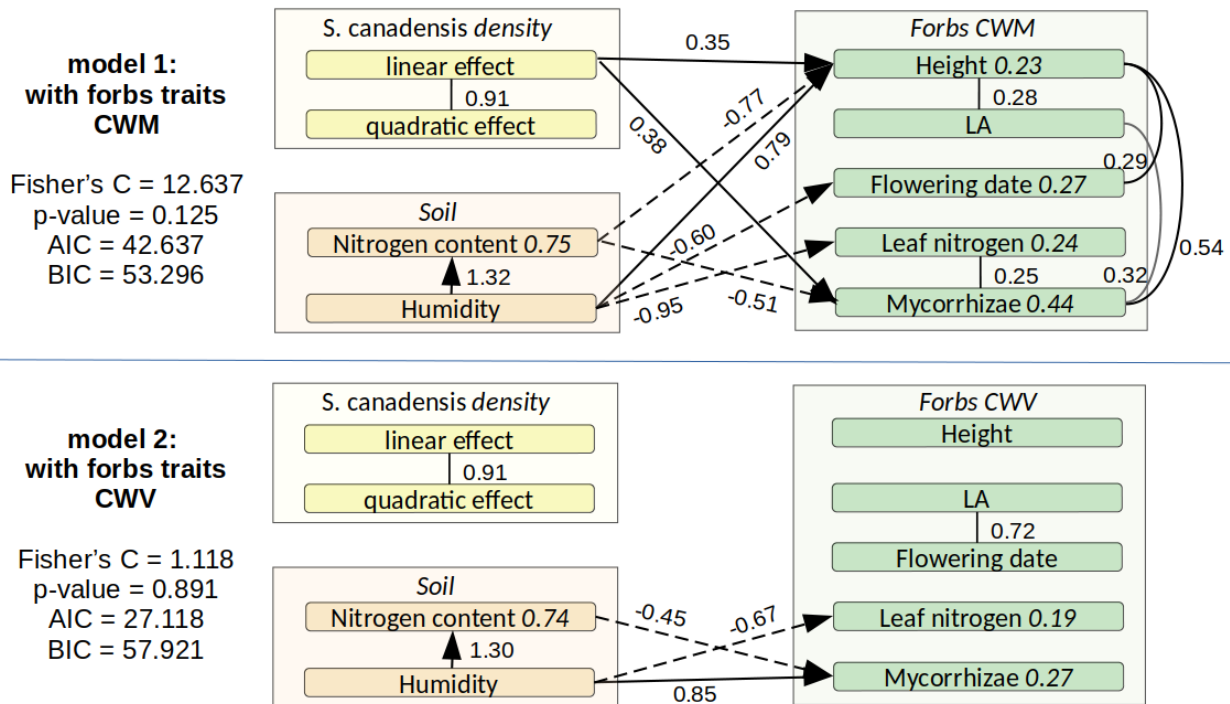
310 The four structural equation models (SEMs) had statistically robust structure (Fisher's C p-  
311 value > 0.45). They revealed no significant relationship between *S. canadensis* density and soil  
312 variables (humidity and N content), and humidity had a positive effect on soil nitrogen content.

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

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

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

324

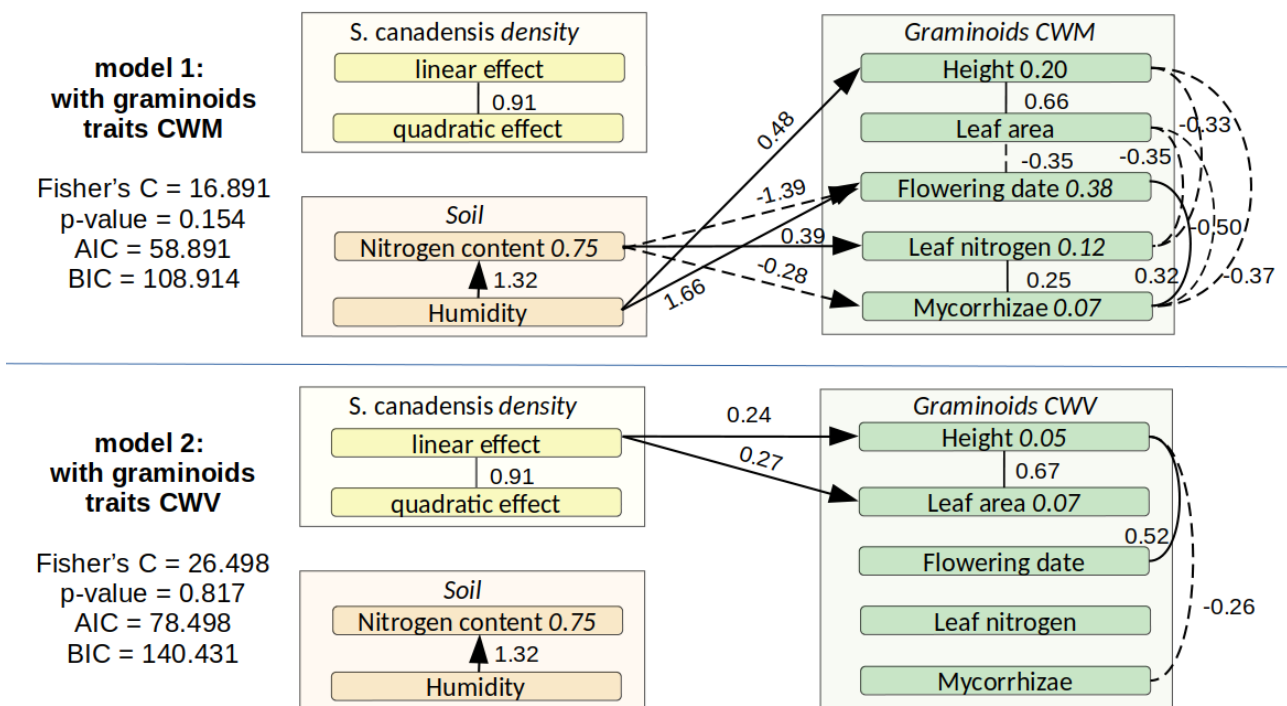


325

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

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

344



345

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

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

355

356

## Discussion

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

371

### **1. Impacts of *S. canadensis* on native species biomass production and diversity: different**

372

### **responses between functional groups**

373 Invasion by *S. canadensis* negatively impacted both forbs and graminoids in terms of biomass  
374 production, taxonomic or functional diversity, but the metrics of diversity that were affected  
375 differed between the two functional groups. These results support the idea that the two functional  
376 groups respond differently to abiotic and biotic constraints (Bowman et al. 1995; Freschet et al.  
377 2018; Raavel et al. 2018) and reveal that one invader can affect different functional groups of plants  
378 via different mechanisms. Importantly, at the community level, we only detected part of the *S.*  
379 *canadensis* effects detected at the functional group level: loss of Biomass production, loss of  
380 Evenness and gain in FDiv. This demonstrates that differences in response to invasion between  
381 functional groups, in terms of taxonomic and functional diversity, can blur signals at the community  
382 level and lead to an underestimation of the impacts of invasions (Münkemüller et al. 2014).

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

## 391 **2. Impacts of *S. canadensis* on native plant traits: resistance strategies differ depending on** 392 **functional groups and constraints**

### 393 **2.1. Competition for light**

394 *Solidago canadensis* is a tall species (up to 2 m), with an abundant foliage all along the stem  
395 and close stems. High densities of *S. canadensis* can thus generate a strong competition to native  
396 species requiring direct light. We detected this constraint for both forbs and graminoids: we

397 observed taller native species at higher invader density. Tall forbs and graminoids are able to  
398 intercept light with their upper parts and are thus less affected by the shade of *S. canadensis*, which  
399 corresponds to an avoidance strategy. Interestingly, in parallel, short graminoids were also  
400 increasingly prevalent along the invasion gradient. This could be due to their naturally good  
401 capacity to tolerate shade, since short species are often under the canopy of native species as well,  
402 corresponding to a tolerance strategy. In addition, short graminoids could benefit from the fact that  
403 they also tend to flower earlier than tall species (due to allometric constraints; Supplementary  
404 materials) and may thus be able to complete their cycle before *S. canadensis* outgrows them (stem  
405 elongation starting in late April and reaching final size late July), corresponding to an escape  
406 strategy. *S. canadensis* also indirectly selects forb species with an early end of flowering that might  
407 be able to escape competition for light, soil nutrients and mycorrhizal interactions.

## 408 **2.2. Competition for soil nutrients and mycorrhizal interactions**

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

421 from that of forbs (different root systems) and they already have low mycorrhizal interactions  
422 (Figure S2).

### 423 **3. Conclusions on the different strategies**

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

### 438 **4. Limits and Perspectives**

439 In invasion studies, it is often difficult to disentangle the causes from the consequences of  
440 invasion (Gallien and Carboni 2017): do the traits of native species in invaded communities reveal  
441 the cause of their invasion (i.e., the driver of their “invasibility”) or their response to the invader  
442 (i.e., a sign of the filtering imposed by the invader)? To avoid this pitfall and isolate only native  
443 species responses to invasion by *S. canadensis*, we selected the meadows of this study to be as  
444 homogeneous as possible in terms of management history, edaphic conditions, and vegetation. In

445 addition, each meadow contained a gradient of invader density independent from any gradient of  
446 edaphic conditions. Therefore, we can assume that prior to the invasion, there was no difference  
447 within the prospected meadows - in terms of community taxonomic and functional structures - that  
448 would explain the current repartition of *S. canadensis*. In other words, the differences we currently  
449 observe along this gradient are likely the result of the effects of the invader, and the density of *S.*  
450 *canadensis* a function of its stage of invasion (not of community invasibility). It should be noted  
451 that we probably underestimated or missed some of these differences because we were not able to  
452 detect plastic responses. Studying trait responses at the species level would be the next step to  
453 improve our understanding of invasion impacts.

454 Another difficulty when studying the impact of invasions on native vegetation is its dynamic  
455 nature. During invasion, the density of the invader increases over time, but native vegetation  
456 responses may take years to appear (Rusterholz et al. 2017). At a given density of the invader, some  
457 native species may show (i) colonization credit (i.e., natives that were locally excluded by dominant  
458 native species before invasion can now colonize sites where *S. canadensis* has replaced these  
459 dominant natives), or (ii) extinction debt (i.e., populations that are currently present in the patch, but  
460 will disappear because their population growth rate is less than one) (Jackson and Sax 2010;  
461 Bagaria et al. 2015; Rumpf et al. 2019). In this study, *S. canadensis* patches were small enough  
462 (<300 m<sup>2</sup>) for the native vegetation to recolonize the patch through a high propagule pressure,  
463 potentially leading to lower colonization credits and higher extinction debts compared to large  
464 invaded areas. Extinction debt was also promoted by the fact that most species in our study site are  
465 perennials: individuals can survive for years even if propagules fail to establish. These dynamic  
466 effects are generally difficult to eliminate, but the fact that colonization credits are limited, while  
467 extinction debts are likely present, tends to make our results more conservative about the magnitude  
468 of *S. canadensis* effects (i.e., we might have missed some mechanisms that are not yet detectable  
469 due to the extinction debt).



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

484

## Conclusion

485 Our study showed that the invader *S. canadensis* has a complex effect on native vegetation. Its  
486 impacts vary between and within functional groups: forbs and graminoids responded to different  
487 constraints and we detected different strategies for resisting the same constraint within graminoids.  
488 Our results show that those native forbs that survive invasion use an avoidance strategy to respond  
489 to increased competition for light, soil nutrients and AMF interactions (i.e. they avoid the stress by  
490 having good abilities to reach the resources), whereas graminoids use all types of resistance  
491 strategies (avoidance, tolerance and escape) to respond to increased competition for light.  
492 Considering traits linked to different constraints and strategies for different functional groups seems  
493 thus essential to understand the complexity of the native vegetation response to invasion. Applying

494 such an approach in future studies may ultimately help us understand why the same invasive species  
495 can have opposing impacts on native communities of different compositions.

496

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## Statements Declarations

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### 1. Data availability statement

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The data used in the analyses are available in the supplementary material. All raw and derived

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data supporting the findings of this study are available from the corresponding author Marie

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Charlotte Grange on request.

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

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### **4. Author Contributions**

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