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► **To cite this version:**

Guillaume Fried, Marta Carboni, Lucie Mahaut, Cyrille Violle. Functional traits modulate plant community responses to alien plant invasion. *Perspectives in Plant Ecology, Evolution and Systematics*, 2019, 37, pp.53-63. 10.1016/j.ppees.2019.02.003 . hal-02411669

HAL Id: hal-02411669

<https://hal.science/hal-02411669>

Submitted on 22 Oct 2021

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1 **Functional traits modulate plant community responses to alien plant**
2 **invasion**

3

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15

16 Declarations of interest: none

17

18 **Abstract (399 words)**

19 It is well known that alien plant invasion modifies the composition and diversity of resident
20 plant communities, yet our ability to predict patterns of vegetation responses to invasion is
21 hampered by a poor understanding of which functional traits make some resident plants more
22 or less vulnerable to invader impacts. For example, resident species may be more likely to
23 persist and coexist with the invader if they display different strategies of resource use (i.e. high
24 niche differences) or if they share similar highly competitive traits (i.e. competitive hierarchy).
25 Here, we used a trait-based approach to 1) specifically test whether species changes in
26 abundance following plant invasion is random or depends on specific functional trait values, 2)
27 identify which functional strategies allow resident species to coexist with the invader and 3)
28 assess to what extent communities where the invader has been removed return to a reference
29 state. To do so, we applied a semi-experimental approach with the annual vine *Humulus*
30 *japonicus*, an invasive species in riparian habitats of Southern France. We monitored plant
31 communities seven times over two years in non-invaded reference plots, invaded plots and
32 removal plots in which the invader had been removed at the seedling stage. We quantified
33 species richness and functional richness as well as mean community trait values of seven traits.
34 The comparison of invaded and removal plots highlighted a strong impact of *Humulus*
35 *japonicus* on both species and functional richness of riparian communities. Resident species
36 that had a distinct flowering onset from the invader faced less pronounced declines.
37 Specifically, species that flowered before the invader reached high cover, and species that had
38 a short flowering duration had lower risk of declining. In addition, species coexisting with the
39 invader when it reached its maximum cover displayed high stature and high seed mass. These
40 results suggest that both *niche differentiation* (in terms of flowering strategy) and *competitive*
41 *hierarchies* (in terms of height and regeneration strategy) play a role in explaining plant
42 community responses to plant invasion. Finally, while species richness recovered rapidly in

43 removal plots, functional richness remained lower than in non-invaded plots, pointing to a state-
44 shift that would otherwise go undetected. Overall, our study highlights that the analysis of the
45 functional traits of both invaders and resident species, combined with regular monitoring over
46 time of non-invaded reference plots, invaded and removal plots can greatly improve our
47 understanding of the impact of plant invasion on resident communities.

48

49 **Keywords:** flowering phenology; functional traits; impact; invasive plants; seed mass;
50 temporal niche

51

52 **Introduction**

53 Research in invasion ecology has gradually shifted from explaining the success of invasive
54 species' to understanding their effects on invaded communities and ecosystems (Vilà et al.,
55 2011). Studies are increasingly finding evidence of strong impacts of invasive plants on plant
56 communities, including species loss and changes in taxonomical composition (Fried et al.,
57 2014; Hejda et al., 2009). Further advances was rendered possible by using functional traits
58 (Castro-Díez et al., 2016; Hejda and Bello, 2013; Jucker et al., 2013), showing that impacts of
59 alien plants are not random and that certain characteristics make some resident species more
60 vulnerable than others (Hejda, 2013; Hejda et al., 2017). However, these studies did not take
61 into account simultaneously the traits of the invasive species and the traits of the resident
62 species in light of the coexistence theory (MacDougall et al., 2009). Here, we contribute to
63 answering one of the basic questions associated with the impacts of invasive species: is it more
64 advantageous for native species to possess characteristics contrasting to the invader (and
65 therefore escape the invader's competition) or to possess similar characteristics and compete
66 with the invader?

67 Trait differences between species are thought to influence biotic interactions and
68 ultimately determine which species can coexist locally (i.e. "biotic filtering") (Weiher et al.,
69 2011). Specifically, according to modern coexistence theory, both *niche differences* and *fitness*
70 *differences* influence competitive outcomes (Chesson, 2000; Kraft et al., 2015). On the one
71 hand, under strong biotic filtering by a dominant invasive alien plant, resident species may
72 persist and coexist with the invader if they possess different traits, reflecting different strategies
73 of resource use (i.e. high niche differences) (Figure 1A, on top). In the same way, resident
74 species with similar traits will be more directly impacted, and as a result of their competitive
75 exclusion, the average trait values of resident species in invaded communities should shift away
76 from the traits of the invader (Figure 1A, at the bottom). On the other hand, species may persist

77 together with the invader if they have similar fitness and equivalent competitive effects (Figure
78 1B, on top), i.e. if they share similar highly competitive traits for resource use (Gallien et al.,
79 2015; Mayfield and Levine, 2010). In this case, it is the species with less competitive traits that
80 will be excluded (e.g. shorter species will be excluded by a taller invader that out-shades them)
81 (Violle et al., 2009). Consequently, if only similarly competitive species (e.g., with similar plant
82 height) coexist with the invader, the average trait values of resident species in the invaded
83 communities will become closer to those of the invader (Figure 1B, at the bottom). Thus,
84 identifying which resident species have persisted and which have been displaced according to
85 their trait values and their differences with those of the invader can unravel the mechanisms
86 underlying coexistence with the invader and the impacts observed (Gallien and Carboni, 2017).

87 From what precedes, the functional structure of the community (i.e., the composition
88 and distribution of functional traits in the community) is expected to be altered as a consequence
89 of plant invasion (Castro-Díez et al., 2016). The impact of biological invasion on the functional
90 structure can be assessed by measuring two major components, which are the range (diversity)
91 and the mean of trait values. First, the functional richness (FRic) is the amount of functional
92 space filled by the community, an equivalent to trait range but in a multidimensional space.
93 Hence, changes in FRic between non-invaded and invaded communities can inform us on
94 whether species loss is associated with a decrease in the range of trait values (Villéger et al.,
95 2008). Second, the community weighted mean (CWM) of a trait is the mean value of that trait
96 across co-occurring species weighted by their abundance (Garnier et al., 2004). The analysis of
97 CWMs of invaded communities is informative in two complementary ways. On the one hand,
98 comparing the CWMs of non-invaded communities with those of the persisting species in
99 invaded communities (i.e. excluding the invader) can help identifying which are the viable
100 strategies for coexistence with the invader. On the other hand, including the invader in the
101 calculation of the CWMs of invaded communities (i.e. the overall final species assemblage) can

102 reveal potential changes in ecosystem functions provided by the community in the post-invasion
103 state (Garnier et al., 2016).

104 So far, most studies quantifying the impacts of invasive species have relied on
105 comparing paired plots of invaded and non-invaded communities (e.g. Castro-Díez et al.
106 (2016); Fried et al. (2014); Jucker et al. (2013)). A much smaller number of studies, have also
107 experimentally removed the invader from the surveyed plots (e.g. Hejda (2012); Hulme and
108 Bremner (2006)). First, removal experiments provide a more direct and less biased measure of
109 impact because removal and invaded paired plots only differ by the presence-absence of the
110 invader, provided the invader is removed at an early stage (Kumschick et al., 2014). Second,
111 when coupled with regular surveys in time, removal plots allow following how communities
112 change after invasion, once the invader is controlled, and whether or not they recover towards
113 a similar state to that of uninvaded reference communities.

114 Here we apply a trait-based approach in order to address the following questions: 1)
115 what is the impact of an invasive plant on the species richness and functional richness of
116 resident communities? 2) Are certain species with particular traits more affected by invasion
117 than others? Does this depend on trait distance to the invader or on trait hierarchies? 3) To what
118 extent communities where the invader has been removed return to a reference state in terms of
119 species and functional richness, and in terms of dominant traits (community weighted means of
120 traits)? To answer these questions, we used a semi-experimental approach with the invasive
121 annual vine *Humulus japonicus* as a model species. Three kinds of plots were compared: 1)
122 invaded plots with high density of the invader, 2) removal plots in invaded sites where the
123 annual vine seedlings were removed early in the season, and 3) still non-invaded plots which
124 are considered as representing the reference state of the habitat before invasion. Comparing
125 these treatments can inform about the impact of the invader (invaded *versus* removal plots) but
126 also about the resilience of restored communities (removal *versus* non-invaded plots).

127

128 **Material and methods**

129 *Study area and habitat*

130 Our experiment was set up along the Gardon River, a tributary of the Rhône, in the
131 Mediterranean region of France (between 44°02'00.16"N, 4°07'53.35"E 43°59'11.93"N,
132 4°12'20.03"E). The Gardon River has a typical Mediterranean-type flow regime characterized
133 by a low mean annual discharge (33 m³/s) with higher flows during winter, extreme seasonal
134 variations, and rapid fluctuations in response to intense rainfall with flood peaks around 100
135 times greater than the mean discharge, usually in autumn (September, October) but occasionally
136 in spring (April) (Dezileau et al., 2014). Riparian vegetation of Mediterranean rivers such as
137 the Gardon River consists in a succession of different communities from herbaceous pioneer
138 communities dominated by *Persicaria lapathifolia*, *Veronica anagallis-aquatica* and *Bidens*
139 *frondosa* (*Bidention* communities) to riparian forests dominated by *Populus alba*. A previous
140 study showed that *H. japonicus* has its optimum in the *Bidention* communities in eutrophic soils
141 and full sun exposure (Fried et al., 2018).

142

143 *Experimental design*

144 We used a hierarchical sampling design with 60 plots nested into four sites: Vézénobres-1
145 (44°02'00.16"N, 4°07'53.35"E), Vézénobres-2 (44°01'56.46"N, 4°08'32.20"E), Ners
146 (44°01'24.77"N, 4°10'02.86"E), Brignon (43°59'11.93"N, 4°12'20.03"E). Invaded plots were
147 chosen at the invasion front downstream of the river (Ners, Brignon) and non-invaded plots
148 were chosen beyond the invasion front upstream of the river (Vézénobres-1, Vézénobres-2).
149 Plots within sites were located 3–500 meters apart from each other. The four sites were located
150 1–10 km apart.

151 In early March 2014, 40 experimental plots were set up at the invasion front in two of
152 the above mentioned sites (Brignon, Ners) where *H. japonicus* was identified as being
153 dominant, based on dense stands of *H. japonicus* seedlings and observations of *H. japonicus*
154 dominance during previous years. In each site, we randomly selected 10 small areas where two
155 paired-1m² permanent subplots were established. The paired subplots were distant 0.5–1.5 m
156 apart from each other, while different pairs were separated by a distance of 2–25 m. Due to the
157 spatial proximity, site conditions are very similar within a pair. Within each pair, we randomly
158 allocated the two treatments: one of the two subplots was left unmanipulated, i.e. invaded by
159 *H. japonicus* (Invaded plots), while in the second one, we removed all seedlings of *H. japonicus*
160 (Removal plots). We assume that removal of small seedlings (~1 cm height in March 2014 and
161 March 2015) of an annual plants resulted in minimal disturbances in the Removal plots
162 (Kumschick et al., 2014). In order to avoid shade effect from adjacent *H. japonicus*, the removal
163 was also applied in a buffer zone of 0.25 m. There were only few later emergences of *H.*
164 *japonicus* (only in April 2014 and April 2015), but we repeatedly had to cut stems of *H.*
165 *japonicus* coming from adjacent areas due to the lateral stem growth of the vine on the ground.

166 Additionally, 20 plots were randomly chosen within two other sites upstream of the river
167 (Vézénobres-1, Vézénobres-2) beyond the invasion front where we presumed that *H. japonicus*
168 has never occurred yet (all presences of *H. japonicus* were downstream of these two sites).
169 Choosing non-invaded reference plots in the same sites where the invader was dominant was
170 not possible as only very few uninvaded areas were left. Therefore, reference sites were chosen
171 based on similar position to the river (distance, topography), similar soil type and similar
172 species pool (vegetation dominated by *Bidens* spp.) compared to the sites used for Invaded and
173 Removal plots. In all plots in all sites we visually estimated cover (to the nearest 5%) of all
174 species at repeated intervals, four times in 2014 (March, April, May, July) and three times in
175 2015 (April, June, August).

176 In order to characterize the invasive species and the resident communities, we used
177 seven traits from different sources: Raunkiær's life forms (annuals, biennials with rosettes,
178 erected perennials, perennials with stolons, perennials with rhizoms or tubers (geophytes), tree
179 seedlings, and vines), flowering onset (month), flowering duration (month) (Julve, 1998),
180 maximum plant height (m) (Tison and De Foucault, 2014), seed mass (g), specific leaf area
181 (SLA, $\text{mm}^2 \cdot \text{mg}^{-1}$) and leaf dry matter content (LDMC, $\text{mg} \cdot \text{g}^{-1}$) (Kleyer et al., 2008). We chose
182 this set of traits because they capture differences in regeneration and acquisition strategies as
183 well as the temporal use and competitive ability for resources in riparian habitats (Garnier et
184 al., 2016).

185

186 *Assessing impact of *H. japonicus* on species and functional richness of resident communities*

187 First, we quantified how *H. japonicus* affected species and functional richness of resident
188 communities. Preliminarily, in order to estimate and compare total species richness (γ richness)
189 in the three treatments (considering all the 20 plots of each treatment), species' accumulation
190 curves were used with the second-order jack-knife method to avoid a negatively biased estimate
191 of species richness (Colwell and Coddington, 1994). Then, at the plot scale, the impact of *H.*
192 *japonicus* on resident communities' diversity was assessed based on species richness (S) and
193 functional richness (FRic). FRic is the amount of functional space filled by the community, an
194 analogue of trait range in a multidimensional space (Villéger et al., 2008). Species richness (S)
195 and functional richness (FRic) across invasion treatments were analyzed using mixed effect
196 models to account for the nested sampling design and the repeated sampling in time in the same
197 plots. Subplot identity (nested within Plots, with Plots nested within Sites) was considered as a
198 random factor on the intercept. Site ("Ners", "Brignon", "Vézénobres-1", "Vézénobres-2"),
199 Treatment ("Invaded", "Removal" and "Non-invaded"), Year (2014 and 2015) and Season, i.e.
200 sampling dates of the consecutive censuses throughout one growing season, and their

201 interactions were included as fixed factors. For species richness S , we used a GLMM with a log
202 link function and we assumed a Poisson distribution error. For FRic, we used a LMM and we
203 assumed a Gaussian distribution error. Plant height and seed mass were log-transformed before
204 the analyses. Starting from the maximum model, we created simplified models and tested with
205 χ^2 the growth of residual deviance associated to the omission of each term or interactions
206 (deletion tests). Given that riverbeds in the study area are strongly colonized by a number of
207 additional alien plants (Chytrý et al., 2008; Fried et al., 2018), models were fitted also using
208 only native species richness (S_{native}) and native functional richness ($\text{FRic}_{\text{native}}$) to assess if the
209 patterns observed for native species follow the same trend as those observed for the whole
210 community. Results were comparable (Appendix A), and in the following, except where noted,
211 we report only the trends based on the entire community. We also developed another series of
212 complementary mixed effect models in order to assess separately the effect of Treatment on S
213 and FRic at the beginning (March 2014) and at the end of the experiment (August 2015) (see
214 Appendix B).

215 These analyses were carried out in the R statistical framework (R Development Core
216 Team, 2008) using package lme4, and post-hoc tests were performed with function lsmeans of
217 package emmeans. Residuals were visually inspected to detect trends that could bias estimates
218 but all assumptions of (G)LMMs were met.

219

220 *Assessing which species and characteristics are most vulnerable*

221 Second, in order to identify the response of individual species to invasion by *H. japonicus*, and
222 whether this response can be explained by trait distances (*niche differentiation*) or trait
223 hierarchies, we computed species abundance (the average cover a species occupied in the plots,
224 A) and species frequency (the number of plots in which a species occurred, Fr) of each species
225 in the Invaded and in the Removal plots. Here we focused on the Invaded-Removal paired plots

226 as they only differ by the presence-absence of the invader and represent therefore the most
227 straightforward and unbiased method to measure the effect of the invader (Kumschick et al.,
228 2014).

229 Preliminarily, to assess the overall changes on resident species abundance and frequency
230 due to the presence of the invader, we compared the average abundance and frequency across
231 all species (i.e., species is the unit of repetition) in Invaded and Removal plots (considering all
232 sampling dates together) using a pairwise Wilcoxon test. Then, for each species, we calculated
233 the Relative Impact (RI) of *H. japonicus* on species frequency and on species abundance, with
234 $RI_x = \frac{x_{Rem} - x_{Inv}}{x_{Rem} + x_{Inv}}$, where x is the variable of interest (frequency or abundance), *Inv* represents the
235 Invaded plots and *Rem* represents the Removal plots (Vila et al., 2006). RI_x ranges between -1
236 (species only in Invaded plots) and 1 (species only in Removal plots). When RI_x is computed
237 by combining all the sampling dates (early spring to late summer, along an increasing cover
238 gradient of *H. japonicus*), this index can detect species that can avoid the maximum
239 development of *H. japonicus* with an early life-cycle (i.e., species that would be equally present
240 in the early censuses of Invaded and Removal plots but absent in late censuses of both types of
241 plots). When computed for the last censuses of the experiment (July 2014 and August 2015,
242 which correspond to the maximum development of *H. japonicus* cover), RI_x will highlight
243 species that are able to coexist with dense stands of the invader.

244 For both temporal scales (all censuses and last censuses), we tested whether the relative
245 impacts of *H. japonicus* on the frequency (RI_{Fr}) and on the abundance (RI_A) of each species
246 were related to their functional distance to *H. japonicus* or to trait hierarchy. For this purpose,
247 we compared two models. In the first, under the niche differentiation hypothesis (Fig. 1A), the
248 explanatory variables consisted for each species in the *absolute* difference of their trait values
249 with *H. japonicus* (i.e., the distance to *H. japonicus*, always positive). In the second model,
250 under the competitive hierarchy hypothesis (Fig. 1B), the explanatory variables consisted for

251 each species in the *relative* difference of their trait value with *H. japonicus* (e.g., a species that
252 is shorter than *H. japonicus* will have a negative value for height difference). We used linear
253 regressions with RI_{Fr} and RI_A of each species as the dependant variables and Raunkiær's life
254 forms and absolute or relative distance of trait values between *H. japonicus* and each species as
255 explanatory variables. Only the species occurring in both Removal and Invaded plots were
256 considered in these analyses (discarded species represented less than 1% of species
257 occurrences).

258

259 *Assessing the impact of H. japonicus on the functional structure of resident communities*

260 The impact on the functional structure was assessed by comparing FRic (see above) and CWMs
261 in the three treatments. Because we were interested in the impact of *Humulus japonicus* on the
262 resident plant communities, we first computed CWMs excluding *Humulus japonicus* to account
263 for shifts of the community *per se* (Thomsen et al., 2016). Second, we computed CWMs
264 including *H. japonicus* to account for potential overall shifts in ecosystem functioning
265 (Thomsen et al., 2016). We compared the CWMs (excluding *H. japonicus*) across treatments at
266 the end of the season when the invader reached its maximum cover (July 2014 and August
267 2015). For this purpose, LMM and deletion tests were used with CWMs as the response
268 variable, Treatment, Site and their interaction as fixed factors and subplot identity as a random
269 factor on the intercept. We expect that CWMs of certain traits in Invaded plots will differ from
270 CWMs in Removal plots and Non-Invaded plots, with values of traits in Invaded plots reflecting
271 viable strategies in invaded sites dominated by *H. japonicus*. Finally, in order to assess to what
272 extent the dominance of *H. japonicus* shift the mean traits of the communities, we repeated the
273 same analysis including *H. japonicus* in the calculation of the CWMs.

274

275 **Results**

276 *Impact on species and functional richness*

277 A total of 179 species were recorded during the two years of the study. Species accumulation
278 curves showed the presence of an asymptote indicating that the sampling was sufficient to
279 capture the majority of the species pool in the three treatments (Appendix C). Estimates of
280 maximum species richness showed that Non-Invaded plots had the greatest richness (154-160),
281 followed by Removal plots (146-154) and Invaded plots (87-94). The functional richness of the
282 cumulated species pool showed less differences between Non-Invaded plots (0.156), Removal
283 plots (0.155) and Invaded plots (0.151).

284 In March 2014, at the beginning of the experiment (before removal), species richness
285 and functional richness of Invaded and Removal paired plots were strongly correlated ($r=0.641$,
286 $P<0.001$, and $r=0.698$, $P<0.001$, respectively), suggesting that there was no bias due to a
287 potential early effect of *H. japonicus* seedlings (see Appendix D). For all 6 subsequent sampling
288 dates there were no more significant correlations between pairs.

289 For the full model (over all the censuses), the marginal r^2 of the GLMM for species
290 richness was 0.773 (while the conditional r^2 was 0.783) indicating that most of the variation of
291 species richness was explained by the fixed factors. Overall, the number of species per plot was
292 significantly different across treatments, across sites, between the two sampling years and there
293 was also a strong effect of season (Table 1). There was no significant interactions between
294 treatment and sites indicating no differences in the effects of invasion in different sites (Table
295 1). There were, however, significant interactions between treatments and season, revealing a
296 different trend across treatments throughout the growing season, and significant interactions
297 between treatments and year reflecting different trends in the two years (Table 1). Similar trends
298 were found with functional richness (Table 1).

299 Species richness first increased in plots of all treatments at the beginning of the season
300 (from March 2014 to April 2014) before a maximum value of species richness was reached in

301 April for both years with a lower level reached in Invaded plots (Table 2, Fig. 2). Then a
302 continuous decline was observed in all plots until the end of the summer with lowest values
303 reached in August 2015 and a sharper decline in Invaded plots (Table 2, Fig. 2). In parallel, the
304 total cover of *H. japonicus* increased throughout the growing season reaching 100% cover in
305 all Invaded plots in August 2015 (Table 2).

306 At the beginning of the experiment (March 2014), species richness varied according to
307 sites ($\chi^2=33.05$ $P<0.001$) and to treatments ($\chi^2=8.55$, $P=0.014$). Species richness was higher in
308 Non-Invaded plots compared to Removal (post-hoc tests, $z=2.80$, $P=0.014$) and Invaded
309 ($z=2.35$, $P=0.049$) plots, while there were no differences between Removal and Invaded plots
310 ($z=0.46$, $P=0.890$, Appendix B). Functional richness differed according to sites (LMM,
311 $\chi^2=14.58$, $P<0.001$) but not according to treatments (LMM, $\chi^2=2.81$, $P=0.246$) (Appendix B).

312 At the end of the experiment (August 2015), species richness varied according to
313 treatments (GLMM, $\chi^2=13.49$, $P<0.001$) but not anymore according to sites (GLMM, $\chi^2=3.73$,
314 $P=0.154$). There were less species in Invaded plots compared to both Removal plots (Tukey
315 Post-hoc test, $z=-6.67$, $P<0.001$) and Non-invaded plots ($z=-7.18$, $P<0.001$) while there were
316 no more differences between Removal plots and Non-invaded plots ($z=2.04$, $P=0.104$,
317 Appendix B). Similarly, functional richness differed among treatments (LMM, $\chi^2=58.60$,
318 $P<0.001$) but not across sites anymore (LMM, $\chi^2=2.02$, $P=0.364$). Functional richness was
319 lower in Invaded plots compared to both Removal plots (Tukey Post-hoc test, $z= -7.45$,
320 $P<0.001$) and Non-invaded plots ($z=-9.96$, $P<0.001$) while there were no more differences
321 between Removal plots and Non-invaded plots ($z= 2.56$, $P= 0.102$, Appendix B). When
322 accounting only for native species in the resident communities, similar results were found for
323 species richness (S_{native}), however native functional richness ($\text{FRic}_{\text{native}}$) remained lower in
324 Removal plots compared to Non-Invaded plots (pots hoc test, $z=3.67$, $P=0.028$).

325

326 *Magnitude of species decrease related to trait distances with the invader*

327 *H. japonicus* reduced average species frequency of occurrence from 8.06% to 3.66% (Wilcoxon
328 paired sign rank test, $V = 9262.5$, $P < 0.001$) and species mean cover from 2.26% to 1.12%
329 (Wilcoxon paired sign rank test, $V = 6677.5$, $P < 0.001$). However the relative ranking of species
330 remained the same for species frequency (Fig. 3a, Pearson's product-moment correlation,
331 $t=30.40$, $r=0.916$, $P < 0.001$) and abundance (Fig. 3b, $t=11.55$, $r=0.706$, $P < 0.001$). Among the
332 native species occurring in both Removal and Invaded-Plots, *Persicaria lapathifolia* showed
333 the strongest decline in frequency (-42%) while *Ficaria verna* or *Alliaria petiolata* were
334 unaffected (species positioned on the 1:1 line on Fig. 3a). *Lythrum salicaria* (-5.4%), *Agrostis*
335 *stolonifera* (-5.1%) and *Galium aparine* (-4.5%) were the native with the strongest decline in
336 cover abundance while *Phalaris arundinacea* was not affected (species positioned on the 1:1
337 line on Fig. 3b).

338 When we considered the *absolute* distance of traits between each species and *H.*
339 *japonicus* (*niche differentiation hypothesis*), linear regressions showed that relative impact of
340 *H. japonicus* on frequency of resident species was negatively correlated with the functional
341 distance of flowering onset and positively correlated with the functional distance of flowering
342 duration (Table 3, Fig. 4a), i.e. resident species displaying the same flowering onset as *H.*
343 *japonicus* were more impacted as well as resident species with different flowering duration.
344 The functional distances of all other traits between resident species and *Humulus japonicus*
345 were not significantly related to the degree of impact (Table 3, Appendix E). When we
346 considered the *relative* distance of traits between each species and *H. japonicus* (*trait hierarchy*
347 *hypothesis*), the results were the same with a positive correlation between the magnitude of
348 impact of *H. japonicus* and the relative distance to flowering onset and flowering duration
349 (Table 3, Fig. 4b) meaning that early flowering species and species with short flowering

350 duration were less impacted than late flowering species and species with long flowering
351 duration.

352 At the end of the season, the magnitude of impact of *H. japonicus* on native species
353 frequency was negatively correlated with their *relative* distance in seed mass (i.e. species with
354 larger seeds than *H. japonicus* were less impacted, Fig. 4c) while no relationships was found
355 with absolute distance of traits (Table 3, Appendix E). There were no significant relationships
356 between the impact of *H. japonicus* on abundance of resident species and the absolute or relative
357 functional distances (Appendix F).

358

359 *Impact on functional structure*

360 Beside the strong shrinkage in trait range revealed by the decrease in FRic, *Humulus japonicus*
361 also shifted the CWMs of invaded communities. At the end of the season of each year (July
362 2014 and August 2015), the persisting species in invaded communities differed from both
363 Removal and Non-Invaded communities, in particular by having a higher CWM for seed mass
364 ($\chi^2=17.4$, $P<0.001$, Fig. 5). They also differed from Removal plots by a later flowering onset
365 (post-hoc test, $t=2.52$, $P=0.041$), a shorter flowering duration (post-hoc test, $t=-3.36$, $P=0.006$),
366 a higher proportion of perennials with rhizomes (post-hoc test, $t=2.68$, $P=0.029$), a higher
367 proportion of vines (post-hoc test, $t=-2.80$, $P=0.021$) and a lower proportion of annuals (post-
368 hoc test, $t=2.61$, $P=0.034$, Fig. 5).

369 In contrast, the overall community CWMs (i.e. including trait values of *H. japonicus*)
370 in invaded plots differed from Removal plots by having higher values for plant height (post-
371 hoc test, $t=5.23$, $P<0.001$), LDMC (post-hoc test, $t=2.96$, $P=0.016$), and lower values for SLA
372 (post-hoc test, $t=-2.97$, $P=0.013$) and flowering duration (post-hoc test, $t=-6.34$, $P<0.001$, Fig
373 6). In addition, invaded communities displayed a lower proportion of perennials with rhizomes
374 or tubers ($\chi^2=13.2$, $P=0.001$), annuals ($\chi^2=8.9$, $P=0.011$), and a higher proportion of annual

375 vines ($\chi^2=192.2$, $P<0.001$) compared to Non-Invaded and Removal plots. The proportion of
376 biennials was also lower compared to Removal plots (post-hoc test, $t=-3.28$, $P=0.006$) while
377 the proportion of stoloniferous perennials was lower than in Non-Invaded plots (post-hoc test,
378 $t=-3.88$, $P=0.023$). Finally, Removal and Invaded plots had a lower proportion of tree seedlings
379 compared to Non-Invaded plots ($\chi^2=11.0$, $P<0.004$, Fig. 6).

380

381 **Discussion**

382 The aim of this study was to improve our understanding of alien species impacts on resident
383 plant communities through a functional lens. Using paired plots (removal versus invaded) as a
384 basis of comparison, we showed a strong impact of *Humulus japonicus* on riparian vegetation
385 communities both taxonomically and functionally. At the landscape scale (γ -diversity) and
386 across all the seven censuses, species richness was reduced by 60% while functional richness
387 only decreased by 3% meaning that species remaining in invaded plots covered most of the
388 functional space of removal plot communities. However, at the plot scale (α -diversity), a
389 stronger decrease, between 77% (July 2014) and 97% (August 2015), was observed for species
390 richness, as well as for functional richness, between 69 % (July 2014) and 100% (August 2015).
391 This is a drastic impact, which can be explained by the high competitive exclusion ability of
392 *Humulus japonicus* (Balogh and Dancza, 2008).

393 The trait values of species able to persist in invaded sites differed from the trait values
394 of species that decrease in presence of the invader. This is remarkable for the traits: flowering
395 onset, flowering duration, seed mass and life form. Perennial species with underground storage
396 organs (rhizoms, tubers) were impacted less than species with an annual life cycle. Using a
397 contrasting life strategy to the annual target invader appears to be an advantage for persisting
398 in invaded sites. A similar result was described by Hejda (2013) who observed that annuals
399 were proportionally more abundant in vegetation invaded by clonal, perennial polycarpic alien

400 plants. Contrary to this, annual vine, i.e. the same life form than the invader, was the second
401 most represented life form strategy in the invaded communities. In this case, it is possible that
402 the resident species using the same strategy than the invader have similar or higher fitness and
403 competitive effects. Besides life forms, the comparison of trait values between persistent and
404 declining species provides arguments in favour of both our hypotheses: niche differentiation-
405 and competitive hierarchies-hypotheses.

406 *Niche differentiation*

407 The decrease in species occurrences in invaded communities was not random, with a strong
408 signal according to the timing of flowering onset of resident species and its overlap with
409 flowering onset of *Humulus japonicus*. Species with a similar flowering onset as *Humulus*
410 *japonicus* were much more impacted compared to species with an earlier life cycle. This
411 suggests that some species can coexist with *Humulus japonicus* in invaded sites if they are able
412 to use resources before the development of the invader, as is the case for early flowering species
413 (e.g. *Alliaria petiolata*, *Cardamine hirsuta*, *Cerastium glomeratum*). These species ended their
414 life cycle before *H. japonicus* reached its full cover. In contrast, species whose flowering onset
415 is similar to that of *H. japonicus* and that share a similar life cycle (spring germination, summer
416 flowering and autumn fruiting) were the most heavily impacted (e.g. *Chenopodium album*,
417 *Persicaria lapathifolia*). This result is in line with the hypothesis that native species need to
418 have a certain degree of niche differentiation to be able to coexist with a strong invader and
419 persist in invaded communities (Shea and Chesson, 2002). It also stresses the importance of
420 traits related to plant phenology: it seems that flowering onset captured well the timing of
421 species occupation of space and the timing of resources use, thus defining species temporal
422 niches (Craine et al., 2012). Apart from competition for space, another hypothesis would be
423 that a similar flowering phenology to the invader exposes resident species to increased
424 competition for pollinator visitation and may lead to reduced seed output and population size

425 (Wolkovich and Cleland, 2011). This hypothesis is however unlikely in the case of *H. japonicus*
426 that is largely pollinated by wind.

427 *Competitive hierarchy*

428 Our study provided evidence that the magnitude of impact on resident species is also associated
429 to trait hierarchies, with less competitive species being more vulnerable. In particular, species
430 that likely had more competitive seedlings than *H. japonicus* because of heavier seed mass,
431 such as *Sicyos angulatus* or *Sambucus ebulus*, were also less impacted by dense stands of *H.*
432 *japonicus*. Heavier seeds may also allow for longer distance dispersal for some species that
433 would be able to co-occur with the invader each year if seeds are replaced in the seed bank from
434 nearby non-invaded populations. However, three other traits known to be related to
435 competitiveness (SLA, growth form and plant height) were also associated with the ability to
436 co-exist with the invader. Although non-significant, we found a similar trend for specific leaf
437 area (SLA), showing that species with faster acquisition ability (higher SLA), such as *Artemisia*
438 *verlotiorum*, *Galium aparine* or *Helianthus tuberosus*, were less impacted by *H. japonicus*. The
439 second approach based on community weighted means showed results consistent with these
440 patterns, with species able to coexist with high cover of *H. japonicus* at the end of the season
441 being mostly tall perennial species, with heavier seeds and late and short flowering times and
442 able to reproduce vegetatively through rhizomes (e.g., *Artemisia verlotiorum*) or tubers (e.g.,
443 *Helianthus tuberosus*). This combination of trait values represents a different strategy than that
444 of *H. japonicus* but resulted in almost similar fitness. In addition, the fact that only species that
445 were taller, capable of lateral spread or that completed their life cycle early in the season (all of
446 which can be considered strategies to avoid competitive shading) were able to persist in invaded
447 communities, supports the idea that competition for light is one of the main mechanisms
448 through which *H. japonicus* reduces germination and establishment of other species beneath its
449 canopy.

450 *Potential impact at the ecosystem level*

451 The non-random impact of *H. japonicus* based on resident species traits, combined with its
452 tendency to become dominant, resulted in a modification of the overall dominant traits of the
453 invaded communities. When including *H. japonicus* in community weighted means
454 calculations, we showed that invaded communities became taller, which suggests potential
455 repercussions on productivity (Lavorel and Garnier, 2002). Flowering duration was overall
456 shorter which can have repercussions on pollinators' communities (Blaauw and Isaacs, 2014).
457 Last but not least, the invasion by *H. japonicus* strongly modified the life-form spectrum of the
458 communities with an annual vine becoming dominant at the expense of a diversity of life forms
459 including annuals, biennials, and different types of perennial species as well as tree seedlings.
460 Displacement of life forms that maintain leaves during the period of floods (e.g., biennials,
461 stoloniferous perennials) can enhance river banks erosion (Tickner et al., 2001). And finally,
462 absence of tree seedlings can also indicate a potential impact on tree recruitment and
463 successional changes in riparian habitats (Flory and Clay, 2010).

464 *Resilience of restored communities*

465 By allowing recruitment from the seedbank or from adjacent sites, Removal plots recovered
466 rapidly the level of species richness observed in Non-Invaded plots. This is consistent with a
467 previous study conducted on riparian habitats in Scotland where, after the invasive *Mumulus*
468 *guttatus* was removed, vegetation recovered rapidly (Truscott et al., 2008). More generally,
469 recover of species richness has also been highlighted in a meta-analysis comparing removal and
470 non-invaded plots using data from restoration studies (Andreu and Vilà, 2011). However,
471 during the same period, removal plots did not reach the same level of native functional richness
472 as non-invaded plots. These results suggest higher functional redundancy (i.e. more species
473 sharing similar functions) in restored communities compared to Non-Invaded communities.
474 Moreover, based on the community weighted means, we observed no full convergence of

475 Removal plots towards Non-Invaded plots. The higher proportion of annual species and the
476 lower LDMC observed in Removal compared to Non-invaded sites exemplifies that plots in
477 Removal sites are dominated by fast growing weedy ruderal species including other invasive
478 alien species (e.g., *Ambrosia artemisiifolia*, *Artemisia annua*). This management-mediated
479 secondary invasion is expected when the removal of an invasive plant species leaves place to
480 bare soils (Gooden et al., 2009) which are typically colonized by species with a ruderal strategy,
481 at least during the first years. Using species number only when assessing the resilience of
482 communities may lead to unreasonably optimistic conclusions while the comparison of trait
483 distribution between removal and non-invaded communities as done here provide a more
484 complete assessment (Hejda et al., 2017).

485

486 **Conclusions**

487 Some previous studies have already highlighted the interest of using a functional approach to
488 understand better the impact of invasive alien plants. However, most of these analyses (e.g.,
489 Hejda, 2013, Hejda et al., 2017) relied solely on multi-site comparative studies that cannot
490 disentangle the invader as a passenger or driver of change in trait distribution of resident
491 communities. Our study is novel as it integrates a functional approach coupled with
492 observational and experimental field approaches, thereby offering greater power in ascertaining
493 the causes and effects of invasion and community change. We opt for contrasting the traits of
494 species able to persist versus species declining in presence of the invader, based on the regular
495 comparison of their frequency of occurrence in removal and invaded plots over time as a more
496 informative approach for measuring the impacts of invasion. Moreover, using functional traits
497 and measuring absolute and relative differences between the invader and resident species allows
498 for testing different hypotheses related to coexistence theory. On the one hand, we found that
499 species that are able to use resources at a different period (mostly before) than the dominant

500 invasive species, can coexist and persist in the same site. On the other hand, we also highlighted
501 that species that display a competitive advantage (high seed mass, perennial with rhizomes or
502 tubers) are also less impacted. Combining these results suggests that 1) whatever their other
503 traits, species that use a different temporal niche can coexist with the invader (*temporal niche*
504 *differentiation*) while 2) the persistence of species that have the same phenology as the invader
505 is contingent on trait values that confer a high competitive ability. The approach developed in
506 this case study can be used more generally to improve the predictions of impact of invasive
507 species on invaded communities and to follow the trajectory of restored communities.

508

509 **Acknowledgments:** The authors thank the Smage des Gardons and Jean-Philippe
510 Reygrobellet for sites access facilities and for funding LM MSc work in 2014. This work was
511 supported by Smage des Gardons and Anses. CV was supported by the European Research
512 Council (ERC) Starting Grant Project “Ecophysiological and biophysical constraints on
513 domestication in crop plants” (Grant ERC-StG-2014-639706- CONSTRAINTS).

514

515 **Authors’ contributions:** GF and LM designed the study and performed the field work in 2014
516 (GF, LM) and 2015 (GF). GF analyzed the data and lead the writing of the manuscript with
517 significant inputs and ideas from MC and CV. All the authors reviewed substantially the
518 manuscript.

519

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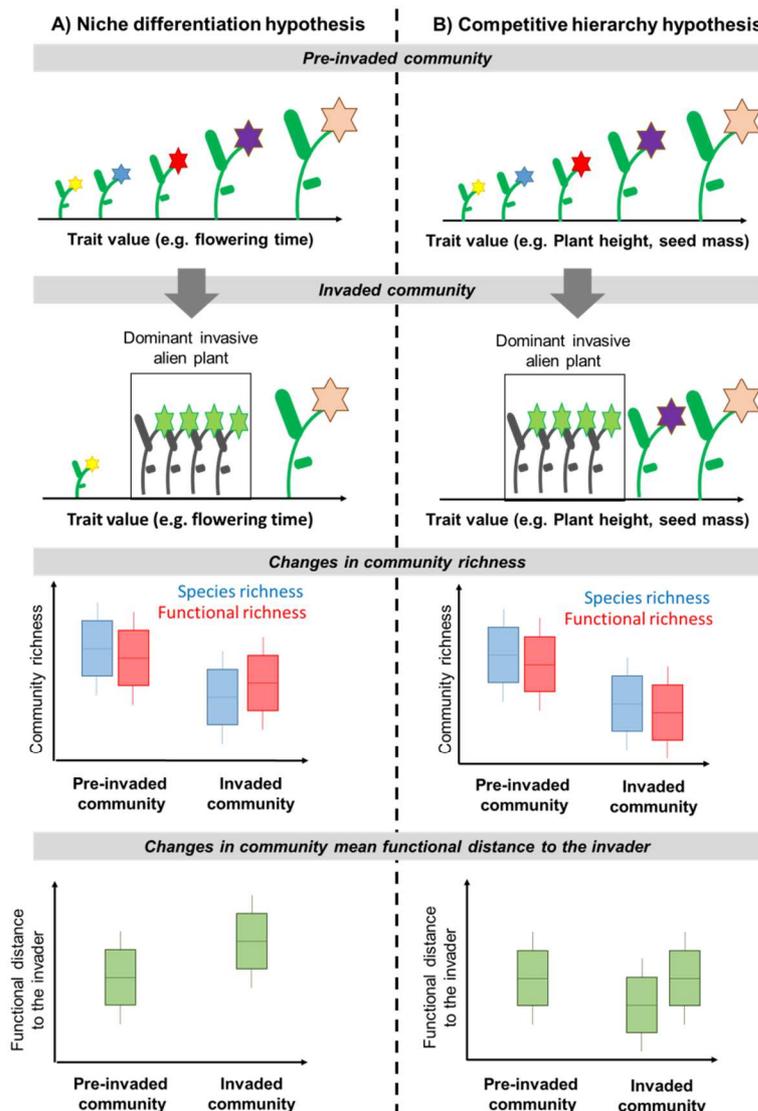
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640

Figure 1. Expected effect of a dominant invasive plant on resident community based on A) the niche differentiation hypothesis or based on B) the competitive hierarchy hypothesis.



Legend:

A) *Niche differentiation hypothesis*: under this hypothesis, resident species that display similar traits than the invader are more impacted, while species displaying different traits can coexist with the invader. Plant invader's establishment decreases species richness and functional richness, but the coexistence of different strategies may limit functional richness decrease. The traits of the resulting invaded community are expected to shift away from the traits of the invader (increased distance).

B) *Competitive hierarchy hypothesis*: the introduction of a tall invasive plant will exclude shorter species by outshading them but species with similar or higher fitness will coexist with the invader. Plant invader's establishment decreases species richness and functional richness. If only similar competitive species (i.e., with similar plant height) coexist with the invader, the average trait values in the invaded communities will become closer to those of the invader. However, similar fitness can be achieved through different combinations of traits. A species with smaller plant height can still coexist with the invader thanks for example to strong lateral spread capacity. In such case, it would be difficult to predict how the average trait values in the invaded communities will shift compare to those of the invader.

Figure 2. Trends in species richness throughout the seasons and years for Removed (Rem.: light grey), Invaded (Inv.: dark grey) and Non-Invaded plots (N.-Inv.: white). For each box plot, top bar is maximum observation, lower bar is minimum observation, top of box is third quartile, bottom of box is first quartile, middle bar is median value and circles are possible outliers.

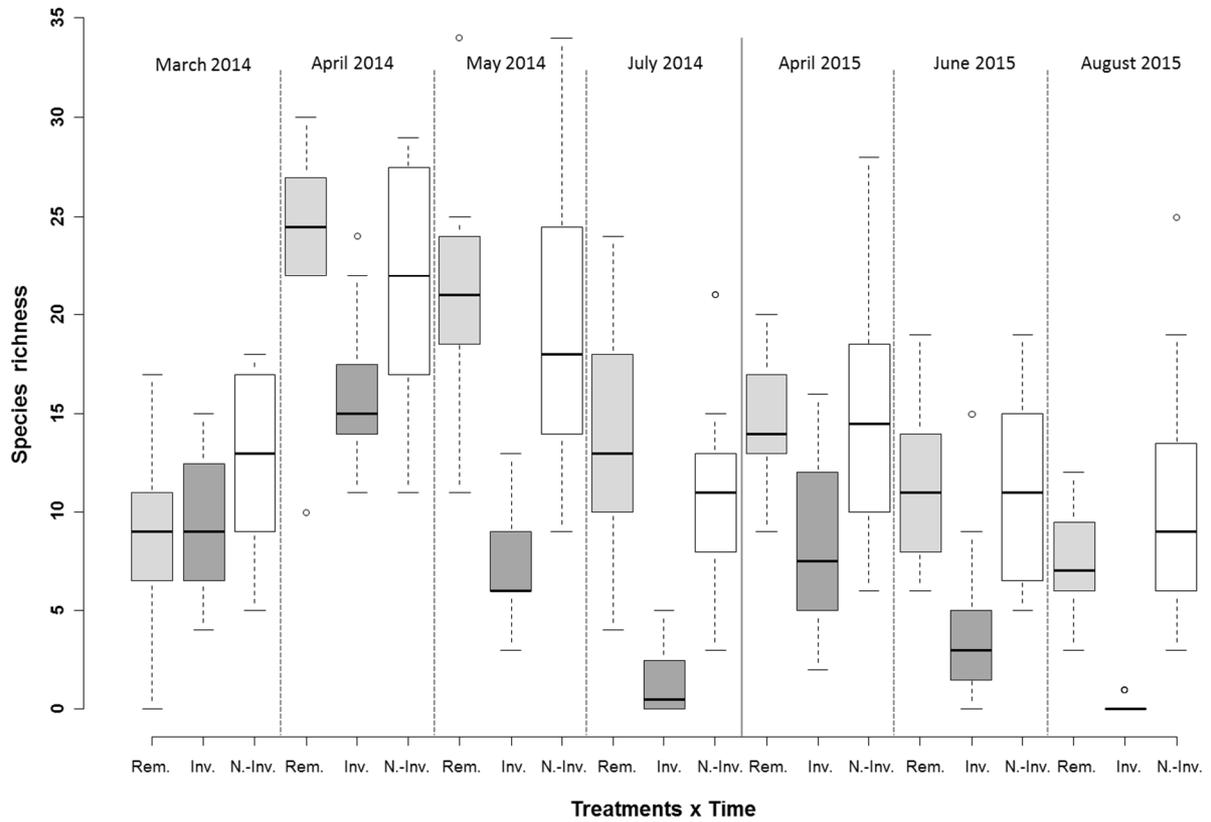


Figure 3. Changes in a) frequency of occurrence and b) abundance (mean cover) between paired Invaded and Removal plots. The red full line represent the 1:1 line, the black dashed line represent the regression slope of $Fr_{Inv.} \sim Fr_{Rem.}$ and $A_{Inv.} \sim A_{Rem.}$. Species names are coded with the first three letters of the genus followed by the first three letters of the species. Only the most common ($Fr > 5\%$) are shown.

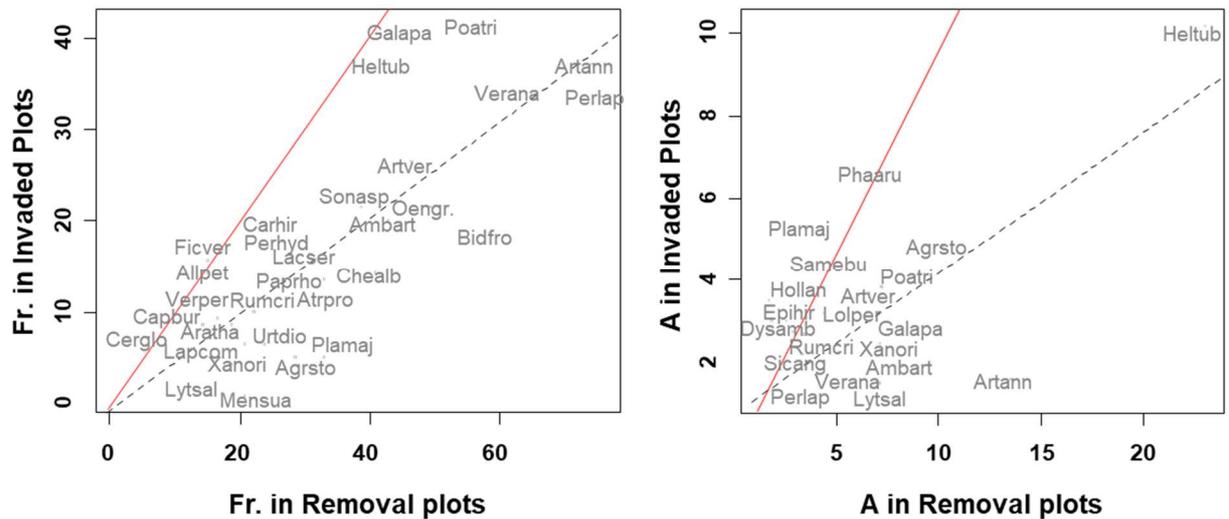
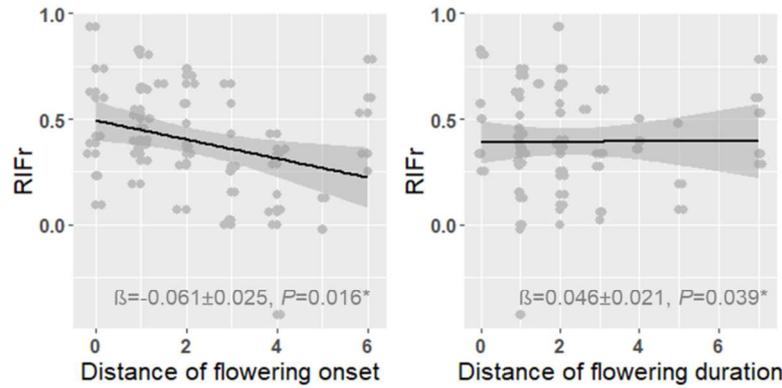
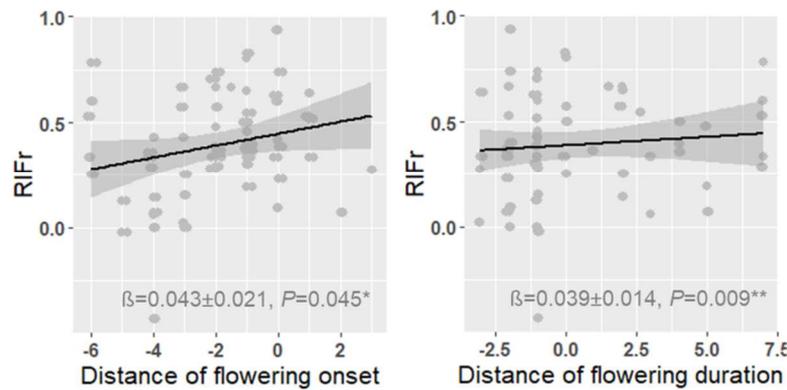


Figure 4. Relationships between the relative impact of *Humulus japonicus* on resident species frequency (RI_{Fr}) and the distance between trait values of the resident species and *Humulus japonicus*. Only significant variable responses are shown (see Table 3 for the detailed results of the linear regressions and Appendix D for all the plots). Each point corresponds to a resident species common to removed and invaded plots. Distances of flowering in month, distance of seed mass in g (log).

a) Absolute functional distance, all censuses



b) Relative functional distance, all censuses



c) Relative functional distance, last censuses (July 2014 & August 2015)

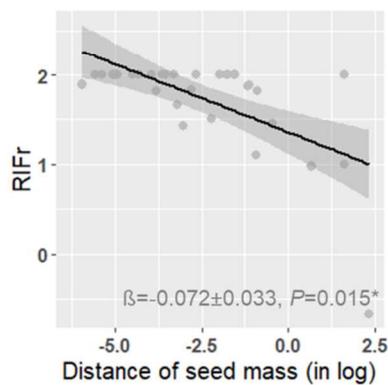


Figure 5. Community-weighted means (CWMs) and proportion of lifeforms at the end of the season without *H. japonicus*. Different letters indicated significant differences of CWMs between treatments according to post-hoc tests. ns: non-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Units: maximum plant height (m), seed mass (g), specific leaf area (SLA, $\text{mm}^2 \cdot \text{mg}^{-1}$), leaf dry matter content (LDMC, $\text{mg} \cdot \text{g}^{-1}$), flowering onset and duration (month). Abbreviations for Raunkiær's life forms: Bis_ros: biennials with rosettes, Erect_Per: erected perennials, Per_Sto: perennials with stolons, Per_rhi_tub: perennials with rhizoms or tubers (geophytes), Tree_seedl: tree seedlings.

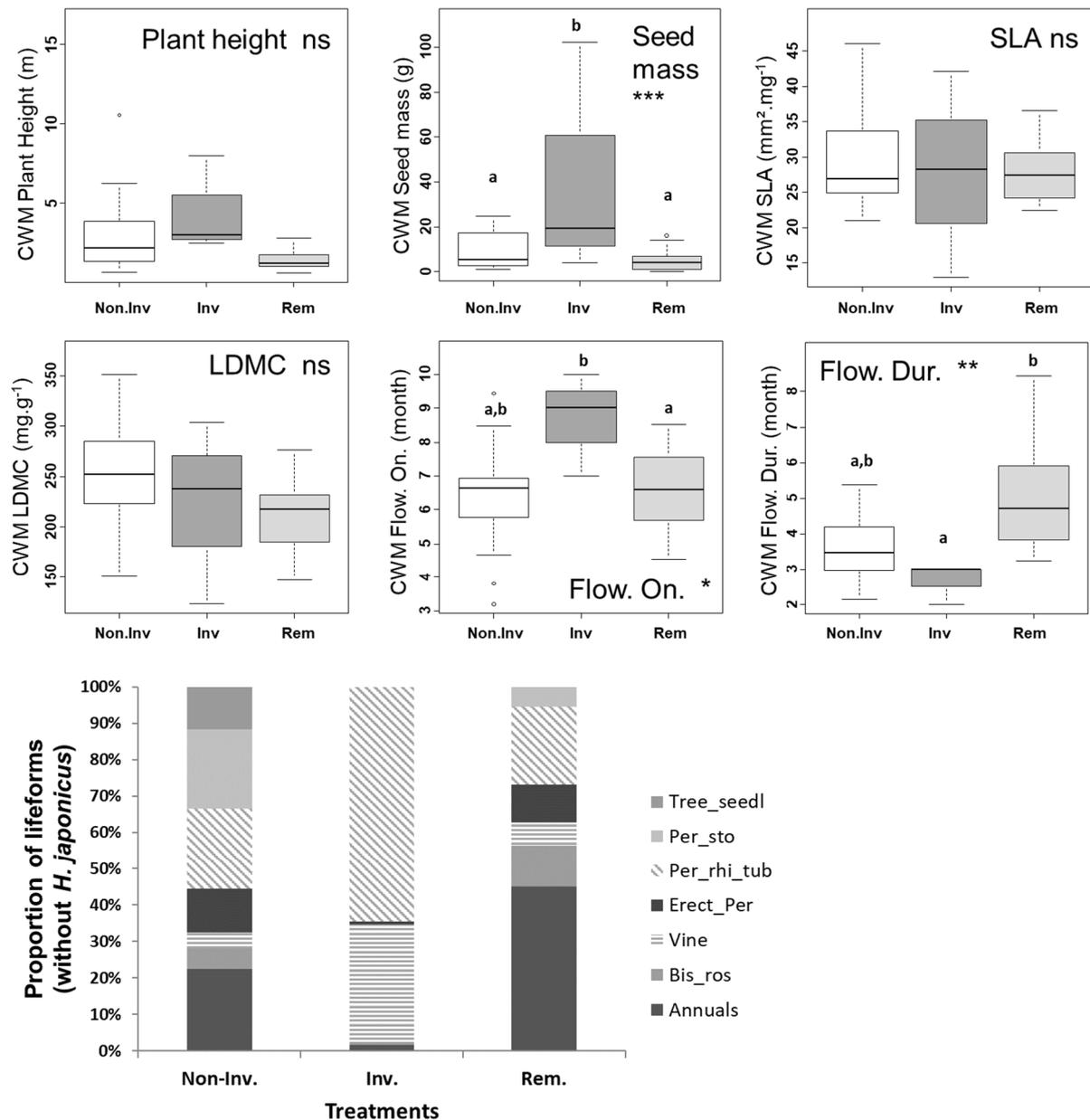


Figure 6. Community-weighted means (CWMs) and proportion of lifeforms at the end of the season with *H. japonicus*. Different letters indicated significant differences of CWMs between treatments according to post-hoc tests. Ns: non-significant, *P<0.05, **P<0.01, ***P<0.001. Units and abbreviations for Raunkiær's life forms: see Figure 6.

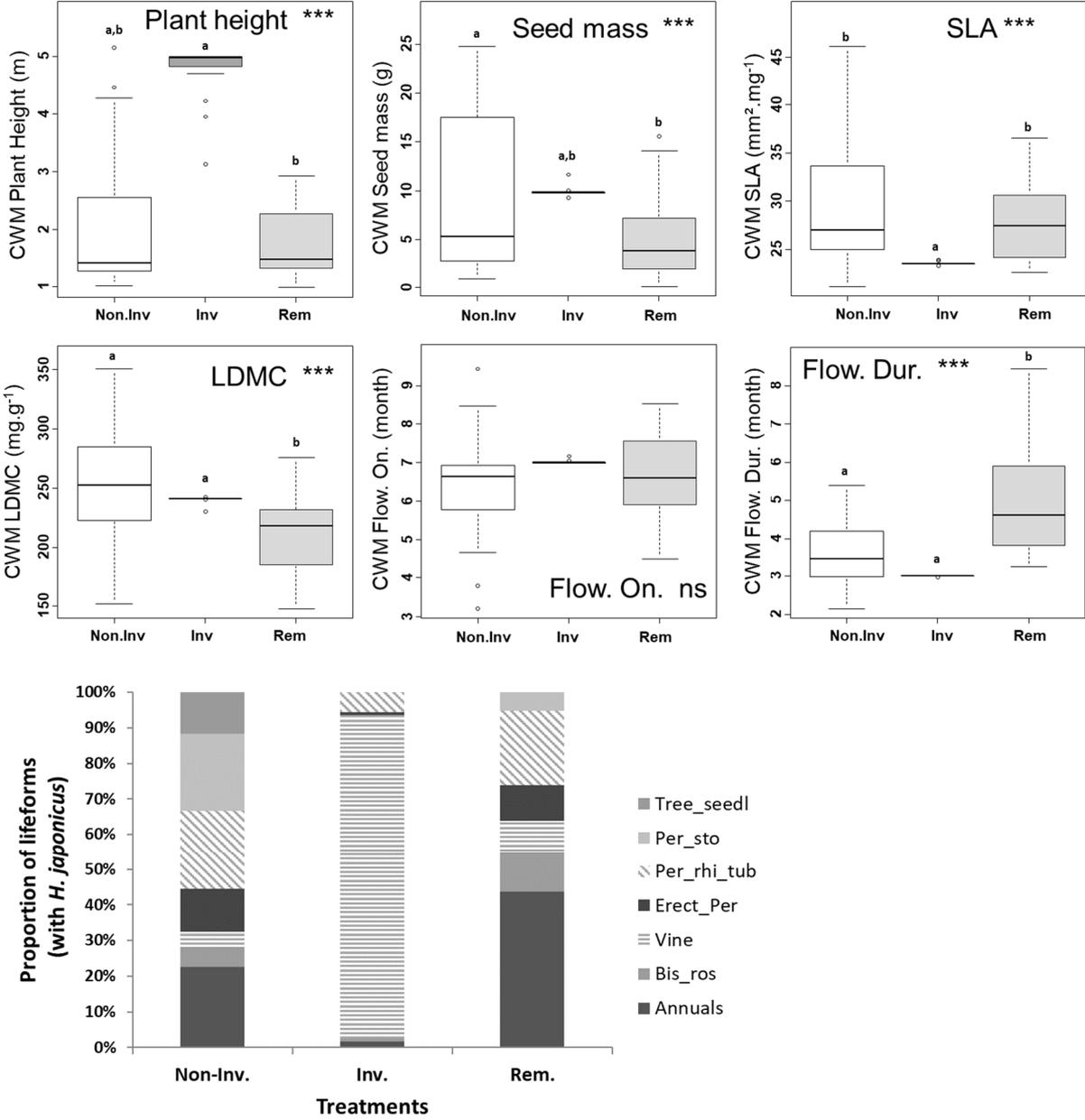


Table 1. Analysis of deviance table of generalized mixed-effect models on species richness and functional richness. For native species richness and native functional richness, see Appendix A.

Factors	Species richness (S)				Functional richness (FRic)			
	deviance	Chisq	df	P	deviance	Chisq	df	P
Treatment	76.5	76.523	2	<0.001	85.9	85.936	2	<0.001
Site	20.5	20.472	2	<0.001	21.0	21.046	2	<0.001
Year	185.9	185.9	1	<0.001	23.5	23.503	1	<0.001
Season	154.2	154.25	1	<0.001	90.8	90.780	1	<0.001
Treatment:Site	3.5	3.4537	1	0.063	0.0	0.0093	1	0.923
Treatment:Year	25.8	25.79	2	<0.001	11.2	11.177	2	0.004
Treatment:Season	207.5	207.5	2	<0.001	34.2	34.221	2	<0.001
Year:Season	56.9	56.899	1	<0.001	11.1	11.141	1	0.001
Treatment:Year:Season	22.8	22.825	2	<0.001	11.5	11.431	2	0.003

Table 2. Mean native and alien species richness and cover of *Humulus japonicus* per treatment and time.

	<i>H. japonicus cover</i>	Native species richness			Alien species richness		
		Invaded plots	Removal plots	Non-invaded plots	Invaded plots	Removal plots	Non-invaded plots
Second week of March 2014	26.65	6.15±2.60	5.55+/-2.72	8.4+/-3.32	3.15+/-1.31	3.25+/-1.89	3.95+/-1.57
Second week of April 2014	52.40	10.8±3.05	16.0+/-3.20	14.74+/-4.16	5.35+/-1.60	8.5+/-1.91	6.9+/-2.47
Second week of May 2014	93.89	4.44±1.89	15.28+/-3.37	13.8+/-5.43	2.65+/-1.73	4.85+/-2.01	5.35+/-2.64
First week of July 2014	94.70	0.6±0.94	7.75+/-3.68	6.85+/-2.54	2.7+/-1.22	6.6+/-2.06	6+/-2.43
Last week of April 2015	44.83	6.33±3.01	10.29+/-2.14	8+/-4.00	1.7+/-1.89	4.3+/-2.30	4.7+/-2.72
Third week of June 2015	89.40	1.95±1.82	6.95+/-2.14	6.26+/-2.35	0.75+/-1.07	5.7+/-2.05	4.2+/-2.59
Third week of August 2015	100.00	0.05±0.22	4.45+/-1.64	5.9+/-3.42	0.15+/-0.37	3.2+/-1.70	4.55+/-2.89

Table 3. Analysis of variance table of the effect of lifeform and functional distance between resident species and *Humulus japonicus* on species changes in relative frequency (RI_{Fr}) for all the censuses and for the last census. Bold values show significant variables.

Functional <i>absolute</i> distance	df	All censuses				Last census (August 2015)			
		Estimate	SS	F-value	P	Estimate	SS	F-value	P
Lifeforms	5	-	0.442	1.749	0.146	-	0.116	0.296	0.908
Plant height	1	-0.060	0.063	1.246	0.271	0.129	0.043	0.547	0.471
SLA	1	-0.001	0.001	0.012	0.913	-0.016	0.138	1.756	0.205
Seed mass	1	0.025	0.063	1.253	0.270	0.063	0.158	2.010	0.177
LDMC	1	-0.000	0.003	0.059	0.810	-0.002	0.079	1.001	0.333
Flowering onset	1	-0.061	0.319	6.313	0.016*	0.083	0.184	2.340	0.147
Flowering duration	1	0.046	0.231	4.574	0.039*	-0.030	0.057	0.725	0.408
Residuals	40		2.023				1.176		
Functional <i>relative</i> distance	df	Estimate	SS	F-value	P	Estimate	SS	F-value	P
Lifeforms	5	-	0.607	2.430	0.052 (.)	-	0.145	0.419	0.828
Plant height	1	0.042	0.026	0.514	0.477	-0.107	0.096	1.626	0.217
SLA	1	-0.002	0.012	0.238	0.628	-0.011	0.254	4.305	0.051 (.)
Seed mass	1	-0.005	0.003	0.059	0.810	-0.072	0.420	7.106	0.015*
LDMC	1	0.000	0.018	0.356	0.554	0.002	0.160	2.705	0.116
Flowering onset	1	0.043	0.213	4.265	0.045*	-0.068	0.125	2.118	0.161
Flowering duration	1	0.039	0.374	7.478	0.009**	-0.016	0.000	0.001	0.972
Residuals	40		1.998				1.037		