



Functional traits modulate plant community responses to alien plant invasion

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ABSTRACT

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

1. Introduction

Research in invasion ecology has gradually shifted from explaining the success of invasive species to understanding their effects on invaded communities and ecosystems (Vilà et al., 2011). Studies are increasingly finding evidence of strong impacts of invasive plants on plant communities, including species loss and changes in taxonomical composition (Fried et al., 2014; Hejda et al., 2009). Further advances were rendered possible by using functional traits (Castro-Díez et al., 2016;

Hejda and Bello, 2013; Jucker et al., 2013), showing that impacts of alien plants are not random and that certain characteristics make some resident species more vulnerable than others (Hejda, 2013; Hejda et al., 2017). However, these studies did not take into account simultaneously the traits of the invasive species and the traits of the resident species in light of coexistence theory (MacDougall et al., 2009). Here, we contribute to answering one of the basic questions associated with the impacts of invasive species: is it more advantageous for native species to possess characteristics contrasting to the invader (and therefore

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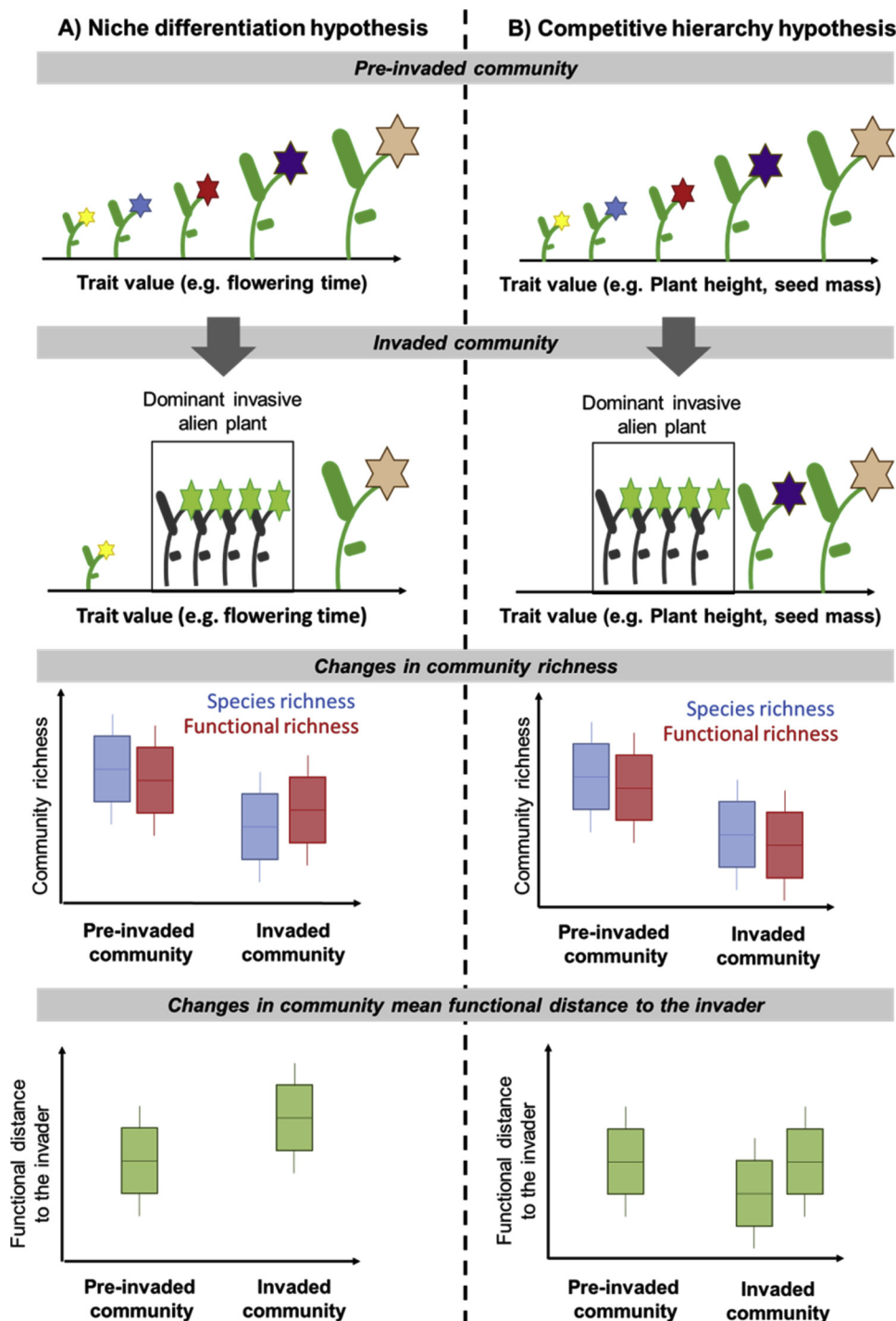


Fig. 1. Expected effect of a dominant invasive plant on resident community based on A) the niche differentiation hypothesis or based on B) the competitive hierarchy hypothesis.

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.

escape the invader's competition) or to possess similar characteristics and compete with the invader?

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

species in invaded communities should shift away from the traits of the invader (Fig. 1A, at the bottom). On the other hand, species may persist together with the invader if they have similar fitness and equivalent competitive effects (Fig. 1B, on top), i.e. if they share similar highly competitive traits for resource use (Gallien et al., 2015; Mayfield and Levine, 2010). In this case, it is the species with less competitive traits that will be excluded (e.g. shorter species will be excluded by a taller invader that out-shades them) (Violle et al., 2009). Consequently, if only similarly competitive species (e.g., with similar plant height) coexist with the invader, the average trait values of resident species in the invaded communities will become closer to those of the invader (Fig. 1B, at the bottom). Thus, identifying which resident species have persisted and which have been displaced according to their trait values

and their differences with those of the invader can unravel the mechanisms underlying coexistence with the invader and the impacts observed (Gallien and Carboni, 2017).

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

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

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

2. Material and methods

2.1. Study area and habitat

Our experiment was set up along the Gardon River, a tributary of the Rhône, in the Mediterranean region of France (between 44°02'00.16"N, 4°07'53.35"E 43°59'11.93"N, 4°12'20.03"E). The Gardon River has a typical Mediterranean-type flow regime characterized by a low mean annual discharge (33 m³/s) with higher flows

during winter, extreme seasonal variations, and rapid fluctuations in response to intense rainfall with flood peaks around 100 times greater than the mean discharge, usually in autumn (September, October) but occasionally in spring (April) (Dezileau et al., 2014). Riparian vegetation of Mediterranean rivers such as the Gardon River consists in a succession of different communities from herbaceous pioneer communities dominated by *Persicaria lapathifolia*, *Veronica anagallis-aquatica* and *Bidens frondosa* (*Bidention* communities) to riparian forests dominated by *Populus alba*. A previous study showed that *H. japonicus* has its optimum in the *Bidention* communities in eutrophic soils and full sun exposure (Fried et al., 2018).

2.2. Experimental design

We used a hierarchical sampling design with 60 plots nested into four sites: Vézénobres¹ (44°02'00.16"N, 4°07'53.35"E), Vézénobres² (44°01'56.46"N, 4°08'32.20"E), Ners (44°01'24.77"N, 4°10'02.86"E), Brignon (43°59'11.93"N, 4°12'20.03"E). Invaded plots were chosen at the invasion front downstream of the river (Ners, Brignon) and non-invaded plots were chosen beyond the invasion front upstream of the river (Vézénobres¹, Vézénobres²). Plots within sites were located 3–500 m apart from each other. The four sites were located 1–10 km apart.

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

Additionally, 20 plots were randomly chosen within two other sites upstream of the river (Vézénobres¹, Vézénobres²) beyond the invasion front where we presumed that *H. japonicus* has never occurred yet (all presences of *H. japonicus* were downstream of these two sites). Choosing non-invaded reference plots in the same sites where the invader was dominant was not possible as only very few uninvaded areas were left. Therefore, reference sites were chosen based on similar position to the river (distance, topography), similar soil type and similar species pool (vegetation dominated by *Bidens* spp.) compared to the sites used for Invaded and Removal plots. In all plots in all sites we visually estimated cover (to the nearest 5%) of all species at repeated intervals, four times in 2014 (March–July) and three times in 2015 (April, June, August).

In order to characterize the invasive species and the resident communities, we used seven traits from different sources: Raunkiaer's life forms (annuals, biennials with rosettes, erected perennials, perennials with stolons, perennials with rhizoms or tubers (geophytes), tree seedlings, and vines), flowering onset (month), flowering duration (month) (Julve, 1998), maximum plant height (m) (Tison and De Foucault, 2014), seed mass (g), specific leaf area (SLA, mm².mg⁻¹) and leaf dry matter content (LDMC, mg.g⁻¹) (Kleyer et al., 2008). We chose this set of traits because they capture differences in regeneration and acquisition strategies as well as the temporal use and competitive ability for resources in riparian habitats (Garnier et al., 2016).

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

First, we quantified how *H. japonicus* affected species and functional richness of resident communities. Preliminarily, in order to estimate and compare total species richness (γ richness) in the three treatments (considering all the 20 plots of each treatment), species' accumulation curves were used with the second-order jack-knife method to avoid a negatively biased estimate of species richness (Colwell and Coddington, 1994). Then, at the plot scale, the impact of *H. japonicus* on resident communities' diversity was assessed based on species richness (S) and functional richness (FRic). FRic is the amount of functional space filled by the community, an analogue of trait range in a multidimensional space (Villéger et al., 2008). Species richness (S) and functional richness (FRic) across invasion treatments were analyzed using mixed effect models to account for the nested sampling design and the repeated sampling in time in the same plots. Subplot identity (nested within Plots, with Plots nested within Sites) was considered as a random factor on the intercept. Site ("Ners", "Brignon", "Vézénobres⁻¹", "Vézénobres⁻²"), Treatment ("Invaded", "Removal" and "Non-invaded"), Year (2014 and 2015) and Season, i.e. sampling dates of the consecutive censuses throughout one growing season, and their interactions were included as fixed factors. For species richness S, we used a GLMM with a log link function and we assumed a Poisson distribution error. For FRic, we used a LMM and we assumed a Gaussian distribution error. Plant height and seed mass were log-transformed before the analyses. Starting from the maximum model, we created simplified models and tested with χ^2 the growth of residual deviance associated to the omission of each term or interactions (deletion tests). Given that riverbeds in the study area are strongly colonized by a number of additional alien plants (Chytrý et al., 2008; Fried et al., 2018), models were fitted also using only native species richness (S_{native}) and native functional richness ($\text{FRic}_{\text{native}}$) to assess if the patterns observed for native species follow the same trend as those observed for the whole community. Results were comparable (Appendix A), and in the following, except where noted, we report only the trends based on the entire community. We also developed another series of complementary mixed effect models in order to assess separately the effect of Treatment on S and FRic at the beginning (March 2014) and at the end of the experiment (August 2015) (see Appendix B).

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

2.4. Assessing which species and characteristics are most vulnerable

Second, in order to identify the response of individual species to invasion by *H. japonicus*, and whether this response can be explained by trait distances (niche differentiation) or trait hierarchies, we computed species abundance (the average cover a species occupied in the plots, A) and species frequency (the number of plots in which a species occurred, Fr) of each species in the Invaded and in the Removal plots. Here we focused on the Invaded-Removal paired plots as they only differ by the presence-absence of the invader and represent therefore the most straightforward and unbiased method to measure the effect of the invader (Kumschick et al., 2014).

Preliminarily, to assess the overall changes on resident species abundance and frequency due to the presence of the invader, we compared the average abundance and frequency across all species (i.e., species is the unit of repetition) in Invaded and Removal plots (considering all sampling dates together) using a pairwise Wilcoxon test. Then, for each species, we calculated the Relative Impact (RI) of *H. japonicus* on species frequency and on species abundance, with $\text{RI}_x = \frac{x_{\text{Rem}} - x_{\text{Inv}}}{x_{\text{Rem}} + x_{\text{Inv}}}$, where x is the variable of interest (frequency or abundance),

Inv represents the Invaded plots and Rem represents the Removal plots (Vila et al., 2006). RI_x ranges between -1 (species only in Invaded plots) and 1 (species only in Removal plots). When RI_x is computed by combining all the sampling dates (early spring to late summer, along an increasing cover gradient of *H. japonicus*), this index can detect species that can avoid the maximum development of *H. japonicus* with an early life-cycle (i.e., species that would be equally present in the early censuses of Invaded and Removal plots but absent in late censuses of both types of plots). When computed for the last censuses of the experiment (July 2014 and August 2015, which correspond to the maximum development of *H. japonicus* cover), RI_x will highlight species that are able to coexist with dense stands of the invader.

For both temporal scales (all censuses and last censuses), we tested whether the relative impacts of *H. japonicus* on the frequency (RI_{Fr}) and on the abundance (RI_A) of each species were related to their functional distance to *H. japonicus* or to trait hierarchy. For this purpose, we compared two models. In the first, under the niche differentiation hypothesis (Fig. 1A), the explanatory variables consisted for each species in the absolute difference of their trait values with *H. japonicus* (i.e., the distance to *H. japonicus*, always positive). In the second model, under the competitive hierarchy hypothesis (Fig. 1B), the explanatory variables consisted for each species in the relative difference of their trait value with *H. japonicus* (e.g., a species that is shorter than *H. japonicus* will have a negative value for height difference). We used linear regressions with RI_{Fr} and RI_A of each species as the dependant variables and Raunkiaer's life forms and absolute or relative distance of trait values between *H. japonicus* and each species as explanatory variables. Only the species occurring in both Removal and Invaded plots were considered in these analyses (discarded species represented less than 1% of species occurrences).

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

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

3. Results

3.1. Impact on species and functional richness

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

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

Removal plots (0.155) and Invaded plots (0.151).

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

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

Species richness first increased in plots of all treatments at the beginning of the season (from March 2014 to April 2014) before a maximum value of species richness was reached in April for both years with a lower level reached in Invaded plots (Table 2, Fig. 2). Then a continuous decline was observed in all plots until the end of the summer with lowest values reached in August 2015 and a sharper decline in Invaded plots (Table 2, Fig. 2). In parallel, the total cover of *H. japonicus* increased throughout the growing season reaching 100% cover in all Invaded plots in August 2015 (Table 2).

At the beginning of the experiment (March 2014), species richness varied according to sites ($\chi^2 = 33.05$, $P < 0.001$) and to treatments ($\chi^2 = 8.55$, $P = 0.014$). Species richness was higher in Non-Invaded plots compared to Removal (post-hoc tests, $z = 2.80$, $P = 0.014$) and Invaded ($z = 2.35$, $P = 0.049$) plots, while there were no differences between Removal and Invaded plots ($z = 0.46$, $P = 0.890$, Appendix B). Functional richness differed according to sites (LMM, $\chi^2 = 14.58$,

$P < 0.001$) but not according to treatments (LMM, $\chi^2 = 2.81$, $P = 0.246$) (Appendix B).

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

3.2. Magnitude of species decrease related to trait distances with the invader

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

Table 2

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

	<i>H. japonicus</i> cover	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

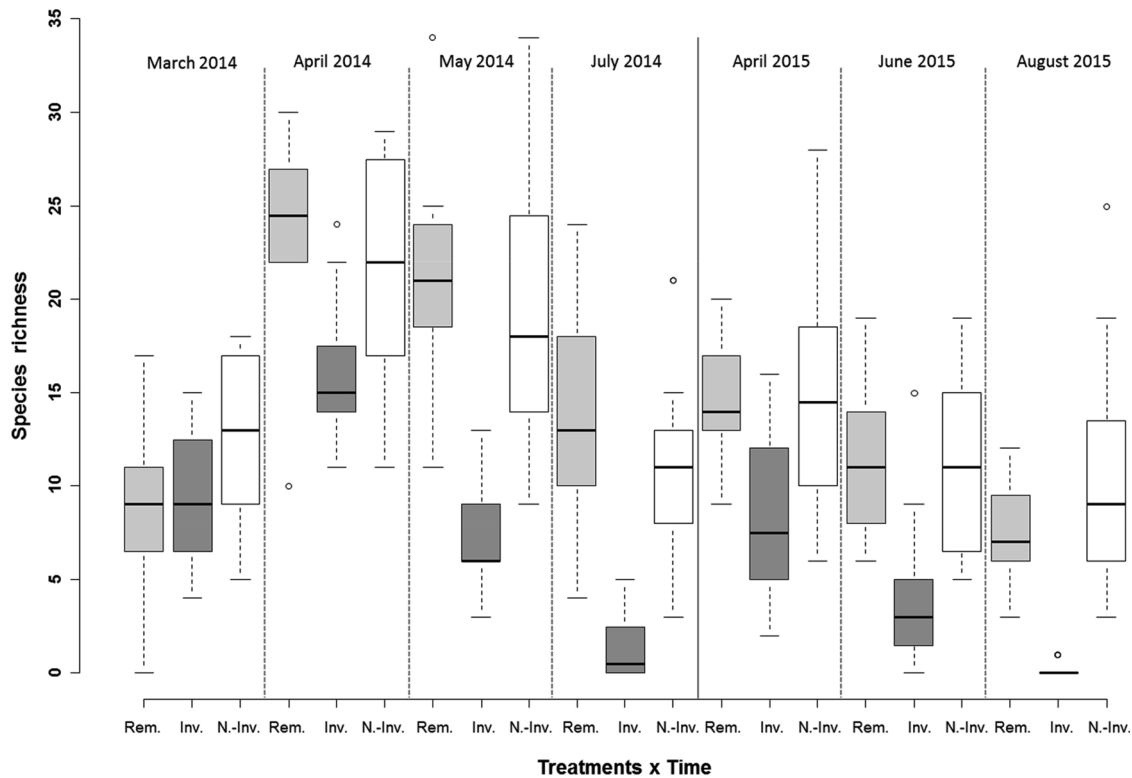


Fig. 2. Trends in species richness throughout the seasons and years for Removed (Rem.: light grey), Invaded (Inv.: dark grey) and Non-Invaded plots (N-Inv.: white). For each box plot, top bar is maximum observation, lower bar is minimum observation, top of box is third quartile, bottom of box is first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

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

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

3.3. Impact on functional structure

Beside the strong shrinkage in trait range revealed by the decrease in FRic, *Humulus japonicus* also shifted the CWMs of invaded communities. At the end of the season of each year (July 2014 and August 2015), the persisting species in invaded communities differed from both Removal and Non-Invaded communities, in particular by having a higher CWM for seed mass ($\chi^2 = 17.4$, $P < 0.001$, Fig. 5). They also

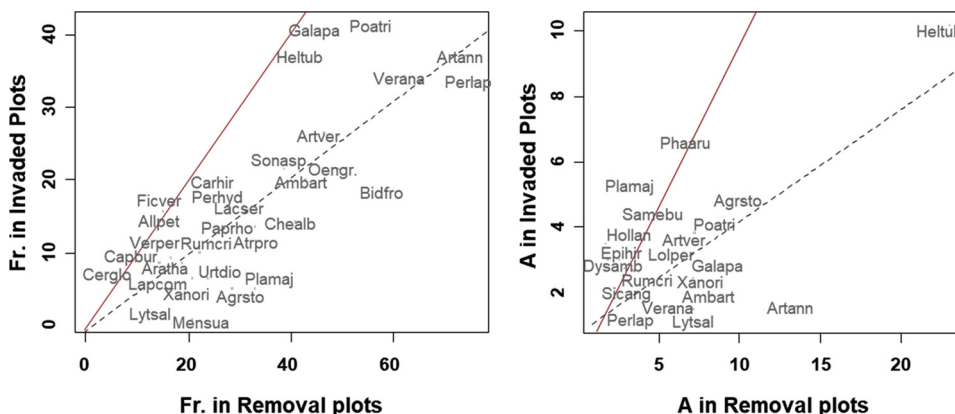


Fig. 3. Changes in a) frequency of occurrence and b) abundance (mean cover) between paired Invaded and Removal plots. The red full line represent the 1:1 line, the black dashed line represent the regression slope of $Fr_{Inv.} \sim Fr_{Rem.}$ and $A_{Inv.} \sim A_{Rem.}$. Species names are coded with the first three letters of the species. Only the most common ($Fr > 5\%$) are shown (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

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_{F_r}) 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		

differed from Removal plots by a later flowering onset (post-hoc test, $t = 2.52$, $P = 0.041$), a shorter flowering duration (post-hoc test, $t = -3.36$, $P = 0.006$), a higher proportion of perennials with rhizomes (post-hoc test, $t = 2.68$, $P = 0.029$), a higher proportion of vines (post-hoc test, $t = -2.80$, $P = 0.021$) and a lower proportion of annuals (post-hoc test, $t = 2.61$, $P = 0.034$, Fig. 5).

In contrast, the overall community CWMs (i.e. including trait values of *H. japonicus*) in invaded plots differed from Removal plots by having higher values for plant height (post-hoc test, $t = 5.23$, $P < 0.001$), LDMC (post-hoc test, $t = 2.96$, $P = 0.016$), and lower values for SLA (post-hoc test, $t = -2.97$, $P = 0.013$) and flowering duration (post-hoc test, $t = -6.34$, $P < 0.001$, Fig. 6). In addition, invaded communities displayed a lower proportion of perennials with rhizomes or tubers ($\chi^2 = 13.2$, $P = 0.001$), annuals ($\chi^2 = 8.9$, $P = 0.011$), and a higher proportion of annual vines ($\chi^2 = 192.2$, $P < 0.001$) compared to Non-Invaded and Removal plots. The proportion of biennials was also lower compared to Removal plots (post-hoc test, $t = -3.28$, $P = 0.006$) while the proportion of stoloniferous perennials was lower than in Non-Invaded plots (post-hoc test, $t = -3.88$, $P = 0.023$). Finally, Removal and Invaded plots had a lower proportion of tree seedlings compared to Non-Invaded plots ($\chi^2 = 11.0$, $P < 0.004$, Fig. 6).

4. Discussion

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

The trait values of species able to persist in invaded sites differed from the trait values of species that decrease in presence of the invader. This is remarkable for the traits: flowering onset, flowering duration, seed mass and life form. Perennial species with underground storage

organs (rhizomes, tubers) were impacted less than species with an annual life cycle. Using a contrasting life strategy to the annual target invader appears to be an advantage for persisting in invaded sites. A similar result was described by Hejda (2013) who observed that annuals were proportionally more abundant in vegetation invaded by clonal, perennial polycarpic alien plants. Contrary to this, annual vine, i.e. the same life form than the invader, was the second most represented life form strategy in the invaded communities. In this case, it is possible that the resident species using the same strategy than the invader have similar or higher fitness and competitive effects. Besides life forms, the comparison of trait values between persistent and declining species provides arguments in favour of both our hypotheses: niche differentiation- and competitive hierarchies-hypotheses.

4.1. Niche differentiation

The decrease in species occurrences in invaded communities was not random, with a strong signal according to the timing of flowering onset of resident species and its overlap with flowering onset of *Humulus japonicus*. Species with a similar flowering onset as *Humulus japonicus* were much more impacted compared to species with an earlier life cycle. This suggests that some species can coexist with *Humulus japonicus* in invaded sites if they are able to use resources before the development of the invader, as is the case for early flowering species (e.g. *Alliaria petiolata*, *Cardamine hirsuta*, *Cerastium glomeratum*). These species ended their life cycle before *H. japonicus* reached its full cover. In contrast, species whose flowering onset is similar to that of *H. japonicus* and that share a similar life cycle (spring germination, summer flowering and autumn fruiting) were the most heavily impacted (e.g. *Chenopodium album*, *Persicaria lapathifolia*). This result is in line with the hypothesis that native species need to have a certain degree of niche differentiation to be able to coexist with a strong invader and persist in invaded communities (Shea and Chesson, 2002). It also stresses the importance of traits related to plant phenology: it seems that flowering onset captured well the timing of species occupation of space and the timing of resources use, thus defining species temporal niches (Craine et al., 2012). Apart from competition for space, another hypothesis would be that a similar flowering phenology to the invader exposes resident species to increased competition for pollinator visitation and may lead to reduced seed output and population size (Wolkovich and Cleland, 2011). This hypothesis is however unlikely in the case of *H. japonicus* that is largely pollinated by wind.

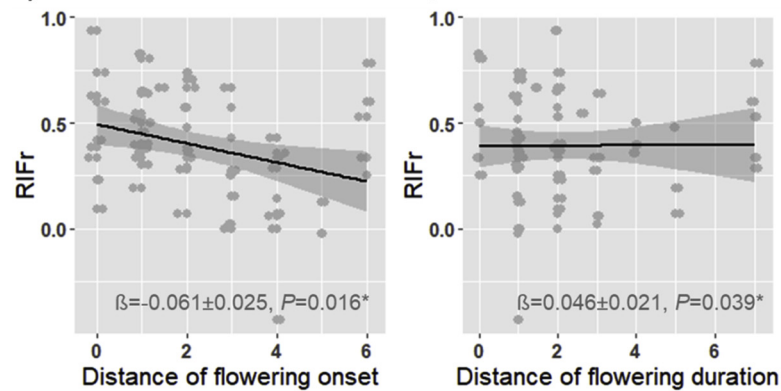
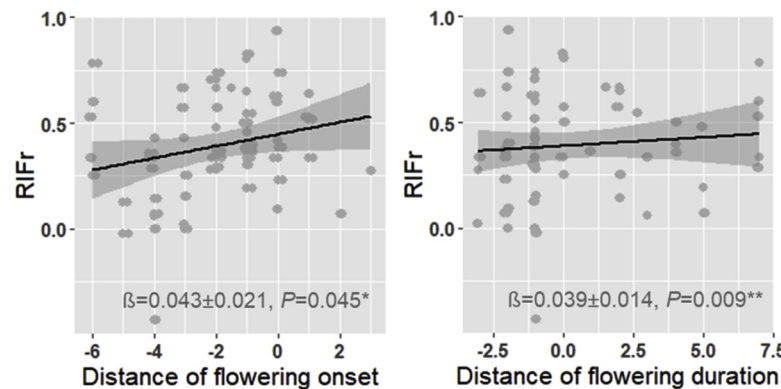
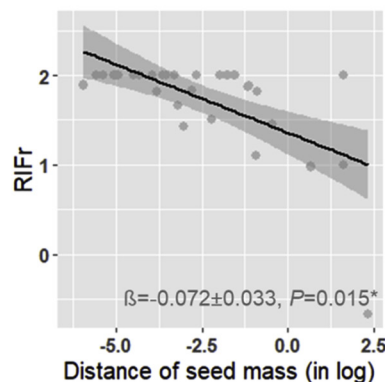
a) Absolute functional distance, all censuses**b) Relative functional distance, all censuses****c) Relative functional distance, last censuses (July 2014 & August 2015)**

Fig. 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).

4.2. Competitive hierarchy

Our study provided evidence that the magnitude of impact on resident species is also associated to trait hierarchies, with less competitive species being more vulnerable. In particular, species that likely had more competitive seedlings than *H. japonicus* because of heavier seed mass, such as *Sicyos angulatus* or *Sambucus ebulus*, were also less impacted by dense stands of *H. japonicus*. Heavier seeds may also allow for longer distance dispersal for some species that would be able to co-occur with the invader each year if seeds are replaced in the seed bank from nearby non-invaded populations. However, three other traits known to be related to competitiveness (SLA, growth form and plant height) were also associated with the ability to co-exist with the

invader. Although non-significant, we found a similar trend for specific leaf area (SLA), showing that species with faster acquisition ability (higher SLA), such as *Artemisia verlotiorum*, *Galium aparine* or *Helianthus tuberosus*, were less impacted by *H. japonicus*. The second approach based on community weighted means showed results consistent with these patterns, with species able to coexist with high cover of *H. japonicus* at the end of the season being mostly tall perennial species, with heavier seeds and late and short flowering times and able to reproduce vegetatively through rhizomes (e.g., *Artemisia verlotiorum*) or tubers (e.g., *Helianthus tuberosus*). This combination of trait values represents a different strategy than that of *H. japonicus* but resulted in almost similar fitness. In addition, the fact that only species that were taller, capable of lateral spread or that completed their life cycle early in the season (all

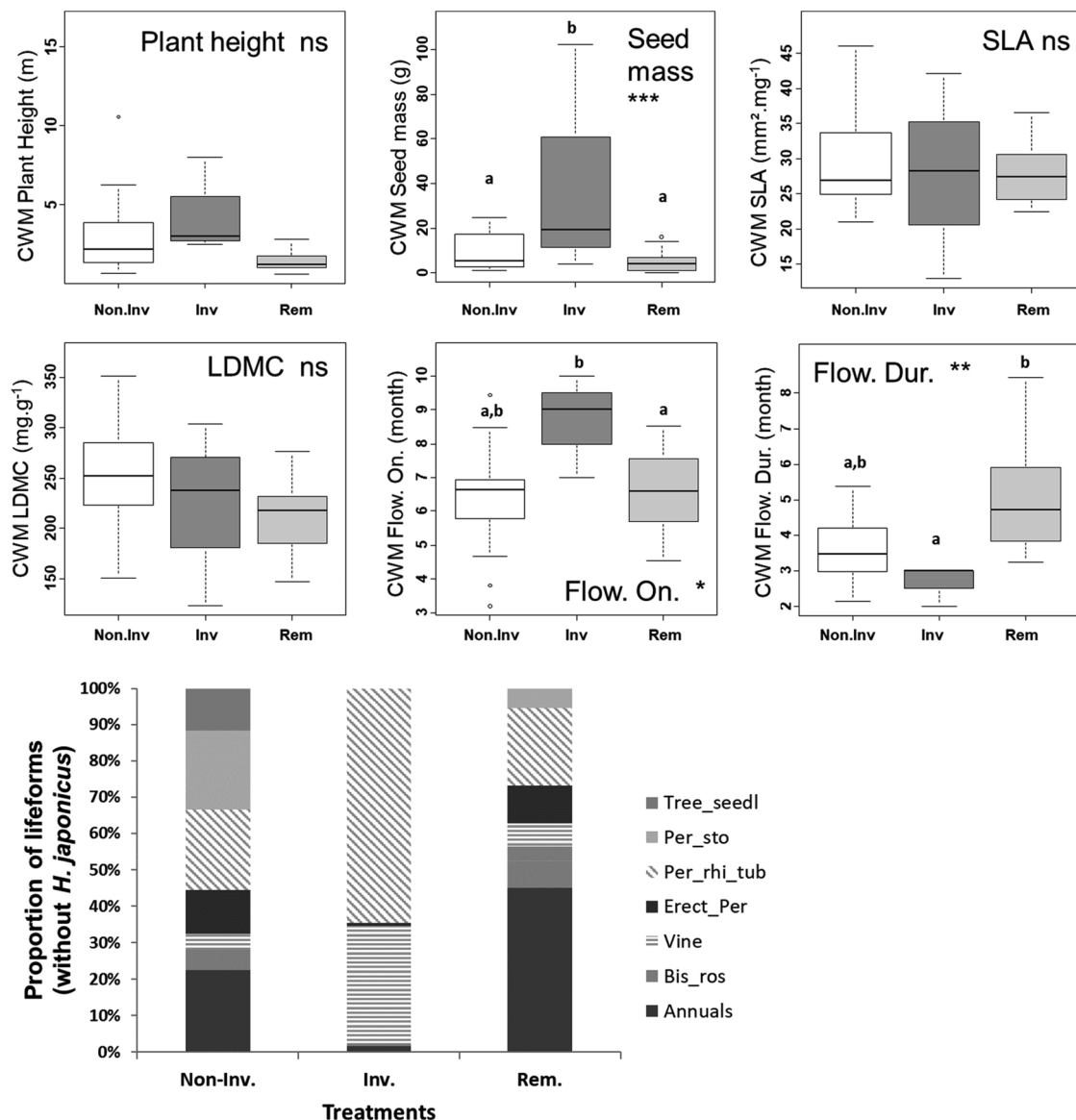


Fig. 5. Community-weighted means (CWMs) and proportion of lifeforms at the end of the season without *H. japonicus*. Different letters indicated significant differences of CWMs between treatments according to post-hoc tests. ns: non-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Units: maximum plant height (m), seed mass (g), specific leaf area (SLA, mm².mg⁻¹), leaf dry matter content (LDMC, mg.g⁻¹), flowering onset and duration (month). Abbreviations for Raunkiaer'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.

of which can be considered strategies to avoid competitive shading) were able to persist in invaded communities, supports the idea that competition for light is one of the main mechanisms through which *H. japonicus* reduces germination and establishment of other species beneath its canopy.

4.3. Potential impact at the ecosystem level

The non-random impact of *H. japonicus* based on resident species traits, combined with its tendency to become dominant, resulted in a modification of the overall dominant traits of the invaded communities. When including *H. japonicus* in community weighted means calculations, we showed that invaded communities became taller, which suggests potential repercussions on productivity (Lavorel and Garnier, 2002). Flowering duration was overall shorter which can have repercussions on pollinators' communities (Blaauw and Isaacs, 2014). Last but not least, the invasion by *H. japonicus* strongly modified the life-form spectrum of the communities with an annual vine becoming

dominant at the expense of a diversity of life forms including annuals, biennials, and different types of perennial species as well as tree seedlings. Displacement of life forms that maintain leaves during the period of floods (e.g., biennials, stoloniferous perennials) can enhance river banks erosion (Tickner et al., 2001). And finally, absence of tree seedlings can also indicate a potential impact on tree recruitment and successional changes in riparian habitats (Flory and Clay, 2010).

4.4. Resilience of restored communities

By allowing recruitment from the seedbank or from adjacent sites, Removal plots recovered rapidly the level of species richness observed in Non-Invaded plots. This is consistent with a previous study conducted on riparian habitats in Scotland where, after the invasive *Mumulus guttatus* was removed, vegetation recovered rapidly (Truscott et al., 2008). More generally, recover of species richness has also been highlighted in a meta-analysis comparing removal and non-invaded plots using data from restoration studies (Andreu and Vilà, 2011).

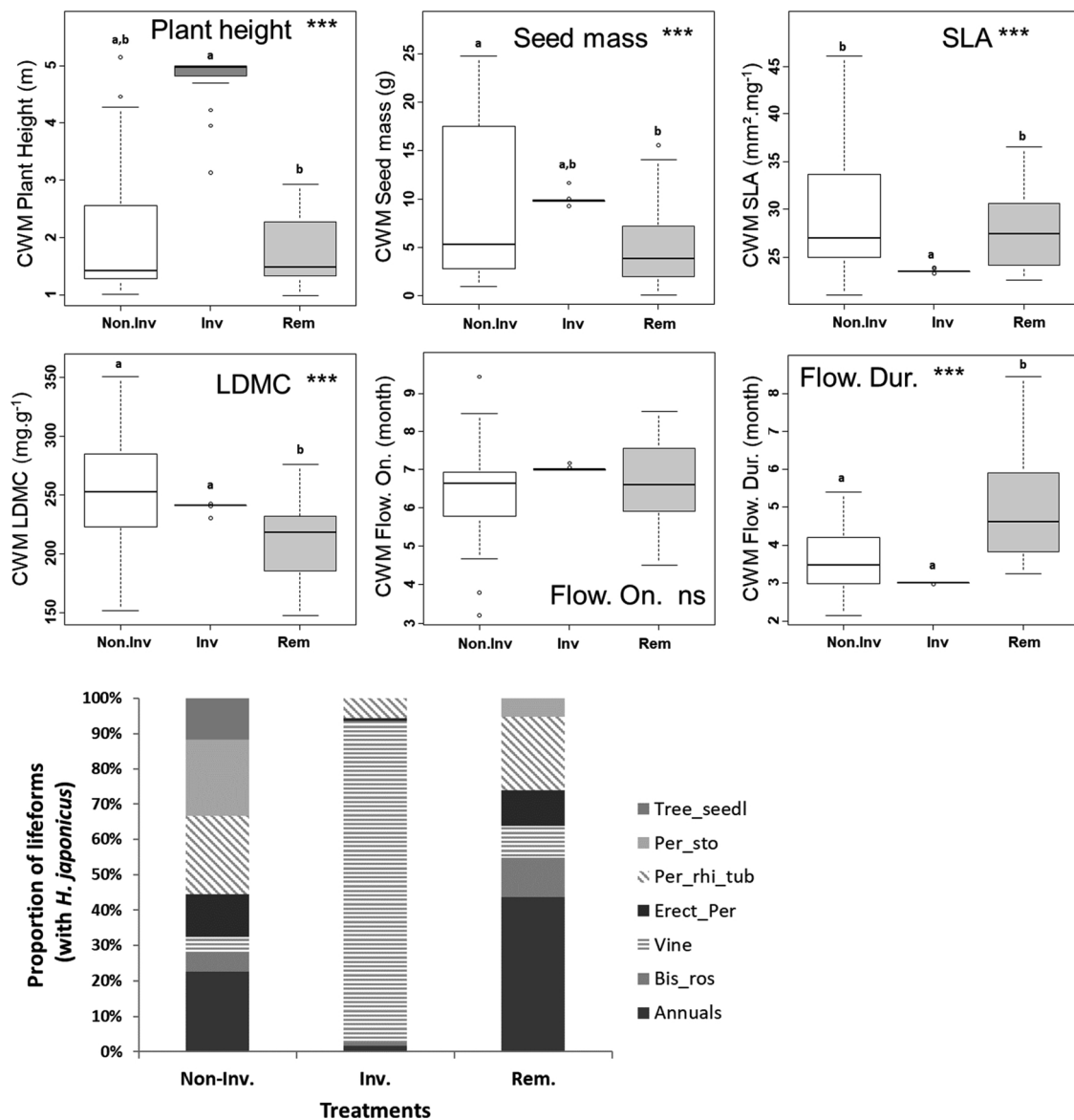


Fig. 6. Community-weighted means (CWMs) and proportion of lifeforms at the end of the season with *H. japonicus*. Different letters indicated significant differences of CWMs between treatments according to post-hoc tests. Ns: non-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Units and abbreviations for Raunkiaer's life forms: see Fig. 5.

However, during the same period, removal plots did not reach the same level of native functional richness as non-invaded plots. These results suggest higher functional redundancy (i.e. more species sharing similar functions) in restored communities compared to Non-Invaded communities. Moreover, based on the community weighted means, we observed no full convergence of Removal plots towards Non-Invaded plots. The higher proportion of annual species and the lower LDMC observed in Removal compared to Non-invaded sites exemplifies that plots in Removal sites are dominated by fast growing weedy ruderal species including other invasive alien species (e.g., *Ambrosia artemisiifolia*, *Artemisia annua*). This management-mediated secondary invasion is expected when the removal of an invasive plant species leaves place to bare soils (Gooden et al., 2009) which are typically colonized by species with a ruderal strategy, at least during the first years. Using species number only when assessing the resilience of communities may lead to unreasonably optimistic conclusions while the comparison of trait distribution between removal and non-invaded communities as done here provide a more complete assessment (Hejda et al., 2017).

5. Conclusions

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

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

Authors' contributions

GF and LM designed the study and performed the field work in 2014 (GF, LM) and 2015 (GF). GF analyzed the data and lead the writing of the manuscript with significant inputs and ideas from MC and CV. All the authors reviewed substantially the manuscript.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ppees.2019.02.003>.

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