



Competition between the invasive *Impatiens glandulifera* and UK native species: the role of soil conditioning and pre-existing resident communities

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Abstract Himalayan balsam (*Impatiens glandulifera*) is a highly invasive annual herb that has become extremely prevalent in riparian zones across the UK. The competitive ability of *I. glandulifera*, both in terms of resource exploitation and allelopathy (i.e., the release of biochemicals that may be toxic to neighbouring plants), is considered a key determinant of its success. Little is known, however, about the effects of the resident community on the establishment and growth of *I. glandulifera*. Here, we aim to increase our understanding of the competitive ability of this highly invasive plant by investigating the effects of soil conditioning on the performance of four co-occurring native species (*Tanacetum vulgare*, *Urtica dioica*, *Chelidonium majus* and *Arabidopsis thaliana*). In addition, we also aim to investigate the effect that the pre-existing species composition have on the performance of *I. glandulifera* seedlings by establishing artificial communities (monocultures and mixtures of four UK native species, including *U. dioica*). We found negative effects of soil conditioning by *I. glandulifera* in all four species, either by reducing above-ground biomass, chlorophyll content or both. Monocultures of *U. dioica* were the only artificial communities that reduced growth of *I. glandulifera*,

and we did not find any support for the idea that a more diverse community may be more resistant to invasion. Our results confirm the high competitive ability of *I. glandulifera* and highlight how the identity of the natives in the resident community may be key to limit its success.

Keywords Activated carbon · Allelopathy · Dominant species · Invasion success · Resident community · Resource exploitation

Introduction

Biological invasions are considered a key driver of global change that can pose a major threat to biodiversity (Vitousek et al. 1997; Pejchar and Mooney 2009; Franklin et al. 2016), but see also Cook-Patton and Agrawal (2014) for evidence of positive effects. Non-native species can negatively affect invaded ecosystems by altering species diversity, community structure and interactions between organisms, which in some cases leads to local extinction of native species (Vilà et al. 2011). Although not yet fully understood, the success of plant invasions seems to depend to a large extent on their interaction with organisms native to the invaded system. For example, invasive plants often exhibit a superior competitive ability in resource use and

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acquisition than natives—even in low resource environments (Funk and Vitousek 2007)—that may explain their dominance (see Gioria and Osborne 2014 and references therein). Superior competitive abilities of invasives over natives may not only relate to resource exploitation, but also to other types of competition, e.g., allelopathy—the release of biochemicals toxic to neighbouring plants (Qin et al. 2013).

Invasion success may also depend on the resident community of plants, and the ‘diversity-invasibility hypothesis’ predicts that high native species richness will increase resistance of ecosystems to invasion (Levine and D’Antonio 1999; Jeschke 2014). In theory, in a species-rich community there is a more complete occupation of most potential niches and more complete and/or efficient uptake of available resources, which would prevent invasion (Elton 1958). However, empirical evidence lacks a consistent diversity-invasibility pattern and supports both direct and inverse relationships between native and exotic species richness (Jeschke 2014; Bjarnason et al. 2017). Contrasting evidence may relate partly to the different spatial scales considered in the studies, with large scales usually supporting a direct relationship and smaller scales an inverse relationship (Fridley et al. 2007). At large scales, environmental heterogeneity and disturbance may promote the coexistence of native and exotic species (Stohlgren et al. 2003, 2006). At small scales, species interactions—including the two above mechanisms (resource competition and allelopathy)—are likely the key drivers determining the invasibility-diversity pattern (Smith and Côté 2019). In addition, patterns of diversity and alien invasion may depend on other aspects—rather than or in addition to species richness—such as the identity of the dominant species in the native community (Funk et al. 2008; Perkins et al. 2011). Native community composition, in terms of presence and/or relative abundance of particular species, may therefore be key to understand patterns of invasion (Emery and Gross 2006, 2007). In fact, significant effects of species identity in promoting or resisting plant invasion have been found (Thomsen and D’Antonio 2007; Emery and Gross 2007; Qin et al. 2013; Zheng et al. 2015), highlighting the relevance of incorporating this latter aspect in future work.

Here, we aim to increase our understanding of the role of competition and native community

composition in the performance of a highly invasive plant in the UK, the Himalayan balsam (*Impatiens glandulifera*). In particular, in this study:

- (1) We aim to investigate the effect of soil conditioning by *I. glandulifera* on the performance of four co-occurring UK native species (*Tanacetum vulgare* L. (Asteraceae), *Urtica dioica* L. (Urticaceae), *Chelidonium majus* L. (Papaveraceae) and *Arabidopsis thaliana* L. (Brassicaceae). In order to reduce the potential interference by allelopathic chemicals in the soil and allow differentiation between the negative effects of allelochemicals and resource competition, all species were planted with and without the addition of finely ground activated carbon to the substrate (see Fig. 1; Callaway and Aschehoug 2000). If allelopathic substances are present in the soil, native species that grow in soil previously used (conditioned) by *I. glandulifera* will have an enhanced performance—in terms of growth and chlorophyll content—when activated carbon is added to the soil (see Vivanco et al. 2004; Prati and Bossdorf 2004). However, if resource competition is stronger than allelopathy, no differences should be observed between growing in soil with and without activated carbon.
- (2) In addition, we also aim to investigate the effect that the pre-existing species composition (monocultures and mixture of four UK native species, including *U. dioica*) has on the performance of *I. glandulifera* seedlings (see Fig. 2). Following the ‘diversity-invasibility hypothesis’ (Levine and D’Antonio 1999; Jeschke 2014) we may expect that *I. glandulifera* will have lower performance—in terms of growth and chlorophyll content—when growing in the mixture of species than in the monocultures.

Materials and methods

Study species

Impatiens glandulifera Royle (Balsaminaceae), the Himalayan balsam, is a highly invasive annual herb, native to the Himalayas and introduced to UK in 1839 (Beerling and Perrins 1993). It is now widespread in

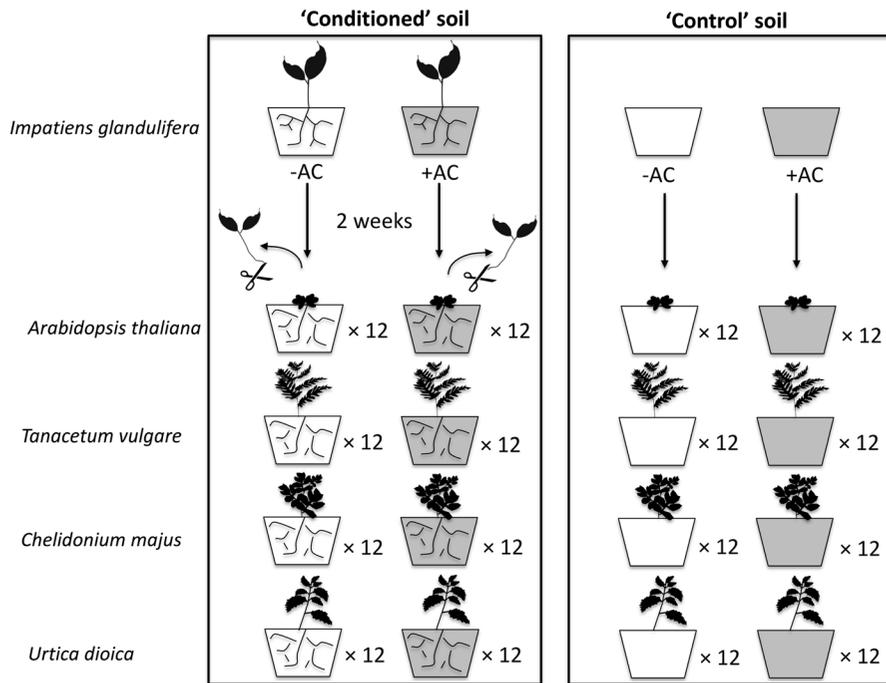


Fig. 1 Schematic representation of the experimental design (Experiment 1), consisting of pots with (+ AC) and without (– AC) activated carbon in the soil that had been ‘conditioned’ or not (‘control’) by growing one individual of *I. glandulifera*. After 2-weeks of growth of the invasive, its above-ground

biomass was removed and one individual of either *Arabidopsis thaliana*, *Tanacetum vulgare*, *Chelidonium majus*, or *Urtica dioica* was grown in each pot. The numbers near the pots indicate the number of replicates per AC (+ AC, – AC) and soil (‘control’, ‘conditioned’) combination

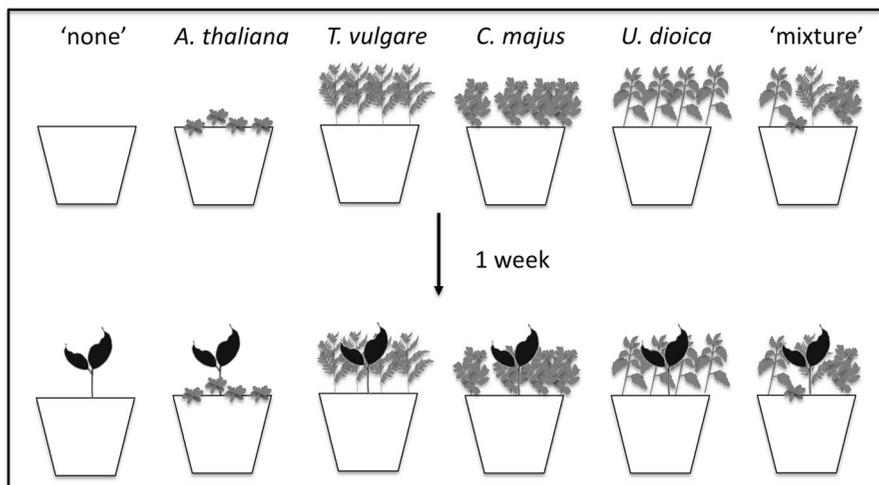


Fig. 2 Schematic representation of the experimental design (Experiment 2). The experiment consisted of 6 different treatments of 10 replicates each: ‘none’, monoculture of ‘*Arabidopsis thaliana*’, ‘*Tanacetum vulgare*’, ‘*Chelidonium majus*’, or ‘*Urtica dioica*’ and ‘mixture’. The treatment ‘none’ consisted of pots that were established without any species.

Monocultures were established by planting 4 individuals of the same species in each pot; mixture was established by planting 1 individual of each of the 4 species. One week after transplanting the native plants, one seedling of *I. glandulifera* was transplanted to each pot

the UK and Europe, and shows high reproductive output (a single plant can produce 800–2500 seeds), rapid growth and high competitive ability (Beerling and Perrins 1993). There is contrasting evidence of the impact of *I. glandulifera* on the species richness and diversity of invaded communities, ranging from negative effects (Hulme and Bremner 2006; Rusterholz et al. 2017; Kiełtyk and Delimat 2019) to weak or even no effects (Hejda and Pyšek 2006; Hejda et al. 2009; Čuda et al. 2017). The allelopathic potential of this species, via naphthoquinones release, has been identified (Ruckli et al. 2014a), together with its ability to disrupt mycorrhizal networks with detrimental effects for native species (Ruckli et al. 2014b, 2016).

Seed origin and germination

Seeds of *I. glandulifera* were collected from three large established populations along the riverbanks (River Taff, Cardiff) in Autumn 2017. A random bulk sample of these seeds was used for this experiment. Seeds were placed on moist filter paper in Petri-dishes and stored in a refrigerator (ca. 4 °C) in darkness for 2-months prior to the start of the experiment in order to break their dormancy requirements.

To assess the effect of *I. glandulifera* on the growth and performance of neighbouring plants, and also to assess the effect of those plants on *I. glandulifera*, we chose three herbaceous perennials: *Tanacetum vulgare* L. (Asteraceae), *Urtica dioica* L. (Urticaceae) and *Chelidonium majus* L. (Papaveraceae) and one annual species: *Arabidopsis thaliana* L. (Brassicaceae). These species were found to co-occur with *I. glandulifera* during field observations in Cardiff, UK. Seeds of the native species were purchased from Nicky's Nursery Ltd (Kent, UK) and sown in germination trays in the glasshouse.

Experimental design

Experiment 1 Effect of soil conditioning by *I. glandulifera* on above-ground biomass and chlorophyll content of native species (see Fig. 1).

Seedlings of *I. glandulifera* were transplanted at the cotyledon stage (approximately 1-week old) to 1L pots (one seedling/pot) filled with a 3:1 soil (Verve multipurpose compost, UK) to sand (Westland horticultural sand, UK) and left to grow for 2 weeks under

glasshouse conditions in Talybont (Cardiff University, Cardiff, UK). Prior to transplanting, activated carbon (AC), NORIT™ SA 2, ACROS Organics™ (Fisher, UK) was added to half of the pots at a rate of 20 ml/L (6 ml per pot). Therefore, there were two different AC treatments: pots without AC (– AC) and with AC (+ AC). Following the 2 weeks, the above-ground biomass of *I. glandulifera* was harvested from a total of 96 pots, which were then used for the ‘conditioned’ soil treatment for assessing the growth of the native species. Our approach using artificial soil aims to avoid confounding factors of natural field-sampled soil, such as differences in soil characteristics (e.g., pH, texture, organic matter) (Pernilla Brinkman et al. 2010).

After germination, seedlings of the native species were transplanted into the pots conditioned by *I. glandulifera*, i.e., where *I. glandulifera* had been previously growing and also to ‘control’ pots, i.e., + AC and – AC pots without previous growth of *I. glandulifera*. The experiment consisted of one species per pot, and there were 12 replicates per each species and AC (+ AC, – AC) and soil treatment (‘control’, ‘conditioned’) combination (total N = 192) (see Fig. 1). Pots were randomly allocated to avoid position-bias within the glasshouse and plants left to grow for 3 weeks.

Three weeks after growing in the experimental conditions, plants of *A. thaliana*, *T. vulgare*, *C. majus* and *U. dioica* were harvested, and their above-ground biomass was oven-dried for 72 h at 65 °C. Then, the above-ground dry mass was weighed with a precision balance in the laboratory (± 0.0001 g). Prior to harvest, we estimated chlorophyll content by measuring three fully developed young leaves with a handheld chlorophyll meter (SPAD-502, Minolta Camera Co., Osaka, Japan), which calculates an index based on absorbance at 650 and 940 nm. SPAD values are well correlated with the chlorophyll content of leaves (Wood et al. 1993; Markwell et al. 1995).

Experiment 2 Effect of species composition on above-ground biomass and chlorophyll content of *I. glandulifera* (see Fig. 2).

After germination, seedlings of the native species were transplanted into 1L pots filled with a 3:1 soil (Verve multipurpose compost) to sand (Westland horticultural sand) mixture. A total of 4 seedlings (either of a single species or a ‘mixture’ of each of the

4 species) were transplanted into each pot. The experiment consisted of establishing 6 different treatments of 10 replicates each: monoculture of '*A. thaliana*', '*T. vulgare*', '*C. majus*', '*U. dioica*', 'mixture', and 'none'. The treatment 'none' consisted of pots that were established without any native species. One week after transplanting the native plants, one seedling of *I. glandulifera* was transplanted to each pot (see Fig. 2). Pots were randomly allocated to avoid position-bias within the glasshouse.

Two weeks after growing in the experimental conditions, the above-ground biomass of *I. glandulifera* was harvested, oven-dried for 72 h at 65 °C and weighed with a precision balance (± 0.0001 g). As above, prior to harvest, we estimated chlorophyll content.

Data Analysis

All data analyses were performed using R version 3.1.2 (R Development Core Team 2014). The effects of 'AC' and 'treatment' on the above-ground dry mass and chlorophyll content of the native plants were analysed using a two-way analysis of variance (ANOVA) by means of the 'aov' function. AC, treatment and their interaction were added as fixed factors to the model. We checked graphically for normality of residuals and homogeneity of variance. The above-ground dry mass for *T. vulgare*, *C. majus*, and *U. dioica* was log-transformed to meet the assumptions of the analysis of variance. The effects of the pre-existing 'species composition' on the above-ground and chlorophyll content of *I. glandulifera* were analysed using a one-way analysis of variance by means of the 'aov' function. The pre-existing 'species composition' was added to the model as fixed factor. We obtained P-values using the 'Anova' function from the 'car package' (Fox and Weisberg 2011) with type III sum of squares. We tested post hoc comparisons between means using Tukey's HSD tests, with $\alpha < 0.05$.

Results

Soil conditioning by *I. glandulifera*: effects on native species

The effects of soil conditioning by *I. glandulifera* on above-ground biomass and chlorophyll content of natives differed between species (see Table 1, Fig. 3). In particular, the above-ground biomass and chlorophyll content were both reduced in *C. majus* (Table 1, T: $P = 0.007$ and $P = 0.004$, respectively; Figs. 3c, 4c) and *U. dioica* (Table 1, T: $P = 0.001$ and $P < 0.001$, respectively; Figs. 3d, 4d). For *T. vulgare*, soil conditioning by *I. glandulifera* reduced the above-ground biomass but did not affect the chlorophyll content (Table 1, T: $P = 0.020$ and $P = 0.549$, respectively; Figs. 3b, 4b). In contrast, the above-ground biomass of *A. thaliana* was not affected, but there was a reduction in chlorophyll content in response to soil conditioning by *I. glandulifera* (Table 1, T: $P = 0.760$ and $P = 0.008$, respectively; Figs. 3a, 4a).

The presence of activated carbon in the soil reduced the above-ground biomass of *A. thaliana* (Table 1, AC: $P = 0.003$, Fig. 3a) and the chlorophyll content of *T. vulgare* (Table 1, AC: $P = 0.012$, Fig. 4b). The interaction of AC and treatment was only significant for *U. dioica* (Table 1, AC \times T: $P = 0.009$); there was no difference in above-ground biomass between control soil and soil conditioned by *I. glandulifera* when activated carbon was added (Fig. 3d). However, there was a significant reduction in the above-ground biomass of *U. dioica* in response to growing in soil conditioned by *I. glandulifera* when soil was not amended with activated carbon (control soil) (Fig. 3d).

Natives species composition: effects on *I. glandulifera*

The above-ground biomass and chlorophyll content of *I. glandulifera* was significantly affected by species composition (Table 2, $P = 0.037$ and $P = 0.013$, respectively). In particular, monocultures of *U. dioica* reduced the above-ground biomass of *I. glandulifera* (Fig. 5a). However, there was no effect on above-ground biomass of the invasive when growing in monocultures of *A. thaliana*, *T. vulgare* and *C. majus* or in the mixture of species (Fig. 5a). Similarly, the chlorophyll content of *I. glandulifera* was reduced

Table 1 Results from the analysis of variance for the effects of AC (activated carbon) and treatment (T) on the above-ground biomass (g) and chlorophyll content (SPAD units) of *Arabidopsis thaliana*, *Tanacetum vulgare*, *Chelidonium majus* and *Urtica dioica*

Species/Source of variation	Parameter							
	Above-ground dry mass (g)				Chlorophyll content (SPAD)			
	df	SS	F	P	df	SS	F	P
<i>A. thaliana</i>								
AC	1	0.0653	9.711	0.003	1	14	1.458	0.234
Treatment (T)	1	0.0006	0.095	0.760	1	74	7.608	0.008
AC × T	1	0.1578	2.346	0.133	1	16	1.666	0.203
Error	44	0.2961			44	425		
<i>T. vulgare</i>								
AC	1	0.0005	0.050	0.824	1	65	6.782	0.012
Treatment (T)	1	0.0565	5.825	0.020	1	4	0.365	0.549
AC × T	1	0.0032	0.334	0.566	1	0.05	0.005	0.941
Error	44	0.4272			44	424		
<i>C. majus</i>								
AC	1	0.0263	3.831	0.057	1	4	0.507	0.480
Treatment (T)	1	0.0553	8.044	0.007	1	77	8.985	0.004
AC × T	1	0.0065	0.952	0.334	1	3	0.401	0.530
Error	44	0.3023			44	375		
<i>U. dioica</i>								
AC	1	0.0049	0.261	0.612	1	13	1.404	0.246
Treatment (T)	1	0.2276	12.209	0.001	1	224	25.098	<0.001
AC × T	1	0.1397	7.493	0.009	1	0.35	0.039	0.843
Error	44	0.8201			44	385		

Values in bold indicate statistical significance at $P \leq 0.05$

when growing with *U. dioica*, and also *A. thaliana*, but no effect was found when growing with any of the other monocultures or in the mixture of species (Fig. 5b).

Discussion

We found negative effects, either in terms of reduced chlorophyll content, reduced above-ground biomass or both, exerted by the invasive on four different co-occurring native species.

The depletion of limiting resources by previous growth of *I. glandulifera* is undoubtedly a major contributing factor in generating these results (Schenk 2006). However, plants can alter subsequent growth by changing soil properties, including not only resource depletion, but more broadly its chemistry, structure and biota (Kulmatiski et al. 2008; van der Putten et al. 2013). So, to what extent these results can be explained beyond resource competition?

Our experimental design aimed at disentangling the effect of resource competition and allelopathy, by the addition of activated carbon. However, results from adding AC were not consistent across species. Although AC has been recommended and used extensively for testing for the effects of allelopathy (Inderjit 2003a, b), its presence has in some cases been found to affect—either increasing or reducing—the growth of plants by modifying nutrient availability (Lau et al. 2008). Here, we found negative effects of AC on *A. thaliana* and *T. vulgare*, which precludes us from obtaining conclusions about allelopathic influence of *I. glandulifera* on these species (Lau et al. 2008). No effects of AC were found for *C. majus*; however, for *U. dioica*, our results suggest a role for allelopathy in contributing to the competitive ability of *I. glandulifera*. Interestingly, the allelopathic effect of *I. glandulifera* has been demonstrated in a previous study with *U. dioica* as a neighbour (Gruntman et al. 2014).

U. dioica was the only species that reduced growth of *I. glandulifera*; however, we did not find any

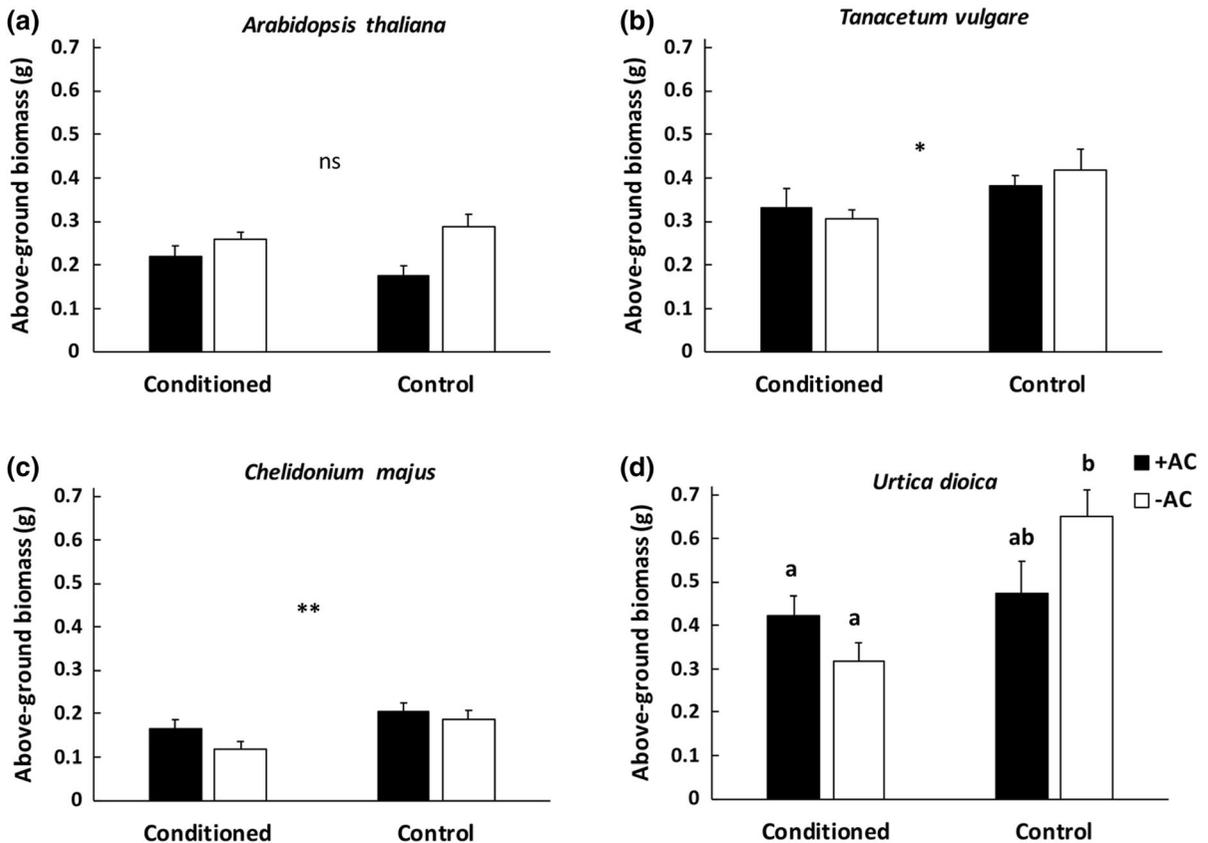


Fig. 3 Above-ground biomass of **a** *Arabidopsis thaliana*, **b** *Tanacetum vulgare*, **c** *Chelidonium majus* and **d** *Urtica dioica* in response to growing in soil ‘conditioned’ or not (‘control’) by *Impatiens glandulifera*, and in presence or absence of activated carbon (+ AC, – AC, respectively). Bars and error bars represent means and SE, respectively (N = 12). Symbols

centred above the bars indicate whether the difference between ‘conditioned’ and ‘control’ soil is statistically not-significant (ns) or significant (* $P < 0.05$, ** $P < 0.01$). In **d** different letters above bars indicate significant differences between groups for the treatment and soil interaction ($P < 0.05$, Tukey’s HSD test)

support for the idea that a more diverse community may be more resistant to invasion (Levine and D’Antonio 1999; Jeschke 2014). The negative effect of *U. dioica* over *I. glandulifera* is not surprising given that it is a highly competitive ruderal species, abundant and dominant in the areas invaded by *I. glandulifera*, where it often forms monospecific stands (Taylor 2009). In fact, negative effects on the growth of *I. glandulifera* have been reported before by young *U. dioica* plants (Bottollier-Curtet et al. 2013) and using *U. dioica* rhizome segments (Tickner et al. 2001). What is perhaps more surprising is that in the current study, individuals of *U. dioica* were at the seedling stage when ‘artificial invasion’ by *I. glandulifera* was imposed. This indicates that the balance between the competitive abilities of the invasive *I.*

glandulifera and *U. dioica* may be affected by the developmental stage of the competing individuals. From our study, it seems that once that *I. glandulifera* is established, this may have negative consequences on *U. dioica*. However, at the same time, our study also suggests that the presence of individuals of *U. dioica*, even at the seedlings stage, may hinder the invasion success of *I. glandulifera*.

The lack of support of our results to the idea that species-rich communities are more resistant to invasion (Elton 1958; Levine and D’Antonio 1999) adds to the studies with contrasting results that found both positive and negative diversity-invasibility relationships (Jeschke 2014; Bjarnason et al. 2017). These studies include both artificial and natural communities, and it has been suggested that artificial

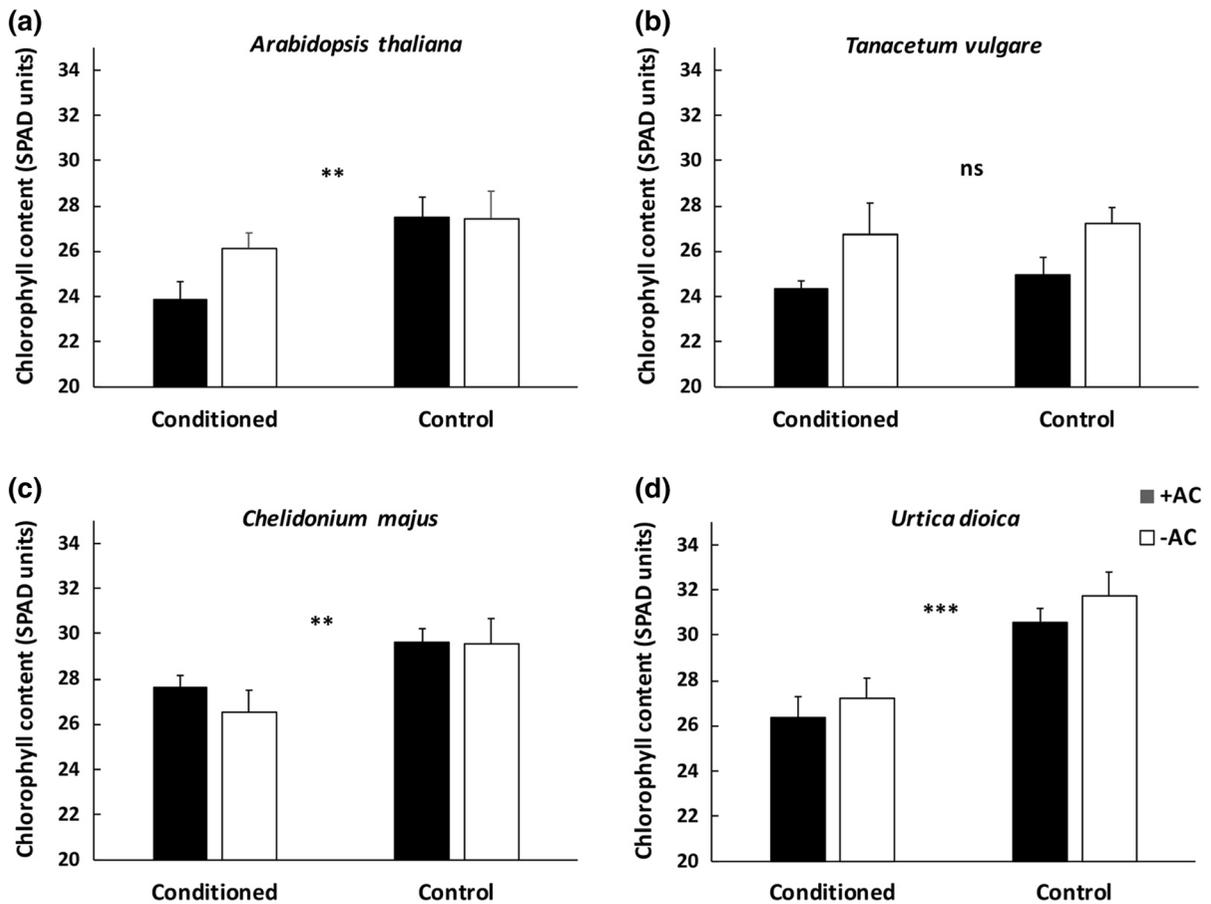


Fig. 4 Chlorophyll content (SPAD units) of **a** *Arabidopsis thaliana*, **b** *Tanacetum vulgare*, **c** *Chelidonium majus* and **d** *Urtica dioica* in response to growing in soil ‘conditioned’ or not (‘control’) by *Impatiens glandulifera*, and in presence or absence of activated carbon (+ AC, – AC, respectively). Bars

and error bars represent means and SE (N = 12), respectively. Symbols centred above the bars indicate whether the difference between ‘conditioned’ and ‘control’ soil is statistically not-significant (ns) or significant (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

Table 2 Results from the analysis of variance for the effects of native species composition (monocultures and mixture of *Arabidopsis thaliana*, *Tanacetum vulgare*, *Chelidonium majus*

and *Urtica dioica*) on the above-ground biomass (g) and chlorophyll content (SPAD units) of *I. glandulifera*

Source of variation	Parameter							
	Above-ground biomass (g)				Chlorophyll content (SPAD)			
	df	SS	F	P	df	SS	F	P
Species	5	0.153	2.58	0.037	5	283	3.23	0.013
Error	52	0.615			52	912		

Values in bold indicate statistical significance at $P \leq 0.05$

communities may be generally young, quite species poor, and structurally simpler—with similar age plants—than natural communities (Zeiter and

Stampfli 2012). In addition, the number of species may not always be the best predictor of how communities function, and several studies have argued about

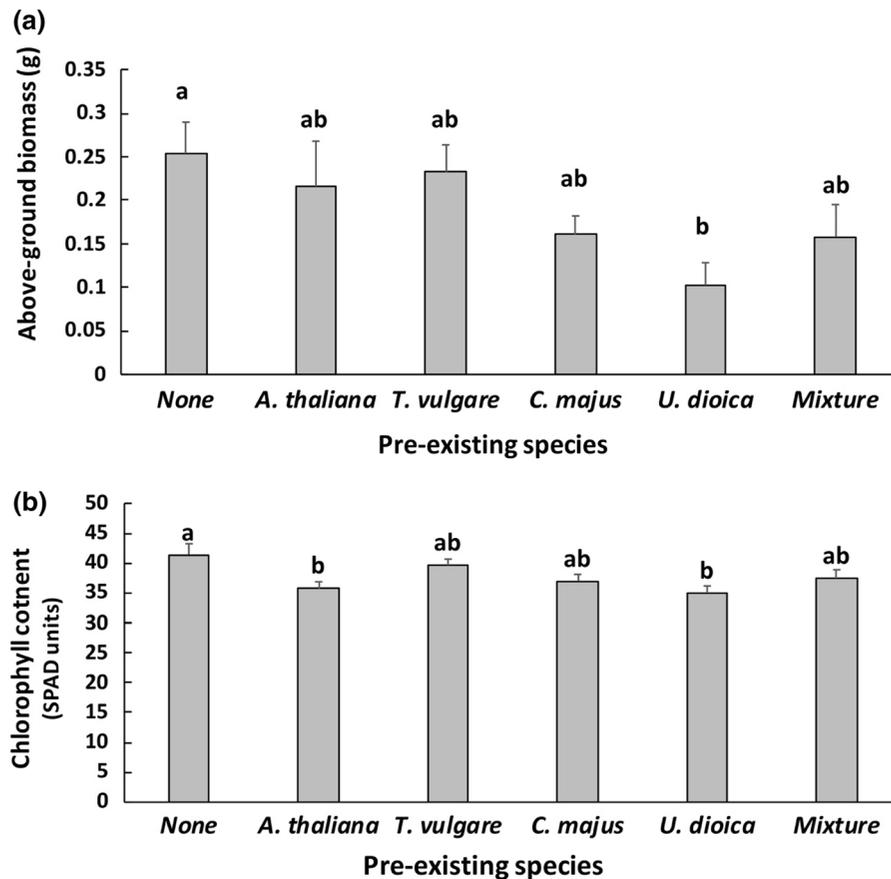


Fig. 5 Above-ground biomass **a** and chlorophyll content **b** of *I. glandulifera* growing 'alone', in previously established monocultures (4 individuals) of '*Arabidopsis thaliana*', '*Tanacetum vulgare*', '*Chelidonium majus*' and '*Urtica dioica*', and in previously established 'mixture' of individuals of these 4

species. Bars and error bars represent means and SE, respectively (N = 12). Different letters above bars indicate significant differences between the different pre-existing species treatment ($P < 0.05$, Tukey's HSD test)

the important role of functional diversity in plant invasion (e.g. Pokorný et al. 2005; Drenovsky et al. 2012; Hejda and de Bello 2013; Castro-Díez et al. 2016). Native species that are functionally similar (e.g., similar Nitrogen acquisition and use, root depth, etc....) to the alien invader will most likely limit the ability of the invader to occupy the resident community by reducing the availability of vacant niches (Drenovsky et al. 2012; Castro-Díez et al. 2016).

Conclusions

Soil conditioned by *I. glandulifera* negatively affected all chosen native species (*A. thaliana*, *T. vulgare*, *C. majus*, *U. dioica*). Negative effects were most likely

mediated through resource competition, however, our results for *U. dioica* also suggest a role for allelopathy in contributing to the competitive ability of *I. glandulifera*. In our artificial communities, monocultures of *U. dioica* were the only ones to reduce the growth of *I. glandulifera*, which may relate to the ruderal and highly competitive ability of this dominant native species. Our results do not support the idea that a more diverse community may be more resistant to invasion. Overall, our results indicate that growth of *I. glandulifera* has negative consequences for native species, and that the identity of the native species in the resident community may be key to limit establishment and therefore the success of *I. glandulifera*.

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References

- Berling DJ, Perrins JM (1993) *Impatiens glandulifera* Royle (*Impatiens* Roylei Walp.). *J Ecol* 81:367–382
- Bjarnason A, Katsanevakis S, Galanidis A et al (2017) Evaluating hypotheses of plant species invasions on Mediterranean islands: inverse patterns between alien and endemic species. *Front Ecol Evol* 5:91. <https://doi.org/10.3389/fevo.2017.00091>
- Bottollier-Curtet M, Planty-Tabacchi A-M, Tabacchi E (2013) Competition between young exotic invasive and native dominant plant species: implications for invasions within riparian areas. *J Veg Sci* 24:1033–1042. <https://doi.org/10.1111/jvs.12034>
- Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290:521–523
- Castro-Díez P, Pauchard A, Traveset A, Vilà M (2016) Linking the impacts of plant invasion on community functional structure and ecosystem properties. *J Veg Sci* 27:1233–1242. <https://doi.org/10.1111/jvs.12429>
- Cook-Patton SC, Agrawal AA (2014) Exotic plants contribute positively to biodiversity functions but reduce native seed production and arthropod richness. *Ecology* 95:1642–1650. <https://doi.org/10.1890/13-0782.1>
- Čuda J, Vítková M, Albrechtová M et al (2017) Invasive herb *Impatiens glandulifera* has minimal impact on multiple components of temperate forest ecosystem function. *Biol Invasions* 19:3051–3066. <https://doi.org/10.1007/s10530-017-1508-z>
- Drenovsky RE, Grewell BJ, D'Antonio CM et al (2012) A functional trait perspective on plant invasion. *Ann Bot* 110:141–153. <https://doi.org/10.1093/aob/mcs100>
- Elton CS (1958) *The ecology of invasion by animals and plants*. The University of Chicago Press, London
- Emery SM, Gross KL (2006) Dominant species identity regulates invasibility of old-field plant communities. *Oikos* 115:549–558
- Emery SM, Gross KL (2007) Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. *Ecology* 88:954–964. <https://doi.org/10.1890/06-0568>
- Fox J, Weisberg S (2011) *An R companion to applied regression*, 2nd edn. Sage, Thousand Oaks
- Franklin J, Serra-Diaz JM, Syphard AD, Regan HM (2016) Global change and terrestrial plant community dynamics. *Proc Natl Acad Sci USA* 113:3725–3734. <https://doi.org/10.1073/pnas.1519911113>
- Fridley JD, Stachowicz JJ, Naeem S et al (2007) The invasion paradox: reconciling patterns and process in species invasions. *Ecology* 88:3–17. [https://doi.org/10.1890/0012-9658\(2007\)88%5b3:TIPRPA%5d2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88%5b3:TIPRPA%5d2.0.CO;2)
- Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079–1081. <https://doi.org/10.1038/nature05719>
- Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. *Trends Ecol Evol* 23:695–703. <https://doi.org/10.1016/j.tree.2008.07.013>
- Gioria M, Osborne BA (2014) Resource competition in plant invasions: emerging patterns and research needs. *Front Plant Sci* 5:501. <https://doi.org/10.3389/fpls.2014.00501>
- Gruntman M, Pehl AKAK, Joshi S, Tielbörger K (2014) Competitive dominance of the invasive plant *Impatiens glandulifera*: Using competitive effect and response with a vigorous neighbour. *Biol Invas* 16:141–151. <https://doi.org/10.1007/s10530-013-0509-9>
- Hejda M, de Bello F (2013) Impact of plant invasions on functional diversity in the vegetation of Central Europe. *J Veg Sci* 24:890–897. <https://doi.org/10.1111/jvs.12026>
- Hejda M, Pyšek P (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biol Conserv* 132:143–152. <https://doi.org/10.1016/j.biocon.2006.03.025>
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J Ecol* 97:393–403. <https://doi.org/10.1111/j.1365-2745.2009.01480.x>
- Hulme PE, Bremner ET (2006) Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. *J Appl Ecol* 43:43–50. <https://doi.org/10.1111/j.1365-2664.2005.01102.x>
- Inderjit Callaway RM (2003a) Experimental designs for the study of allelopathy. *Plant Soil* 256:1–11
- Inderjit Nilsen ET (2003b) Bioassays and field studies for allelopathy in terrestrial plants: progress and problems. *CRC Crit Rev Plant Sci* 22:221–238. <https://doi.org/10.1080/713610857>
- Jeschke JM (2014) General hypotheses in invasion ecology. *Divers Distrib* 20:1229–1234. <https://doi.org/10.1111/ddi.12258>
- Kiełtyk P, Delimat A (2019) Impact of the alien plant *Impatiens glandulifera* on species diversity of invaded vegetation in the northern foothills of the Tatra Mountains, Central Europe. *Plant Ecol* 220:1–12. <https://doi.org/10.1007/s11258-018-0898-z>
- Kulmatiski A, Beard KH, Stevens JR, Cobbold SM (2008) Plant-soil feedbacks: a meta-analytical review. *Ecol Lett*

- 11:980–992. <https://doi.org/10.1111/j.1461-0248.2008.01209.x>
- Lau JA, Puliafico KP, Kopshever JA et al (2008) Inference of allelopathy is complicated by effects of activated carbon on plant growth. *New Phytol* 178:412–423. <https://doi.org/10.1111/j.1469-8137.2007.02360.x>
- Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15–26
- Markwell J, Osterman JC, Mitchell JL (1995) Calibration of the Minolta SPAD-502 leaf chlorophyll meter. *Photosynth Res* 46:467–472. <https://doi.org/10.1007/BF00032301>
- Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. *Trends Ecol Evol* 24:497–504. <https://doi.org/10.1016/J.TREE.2009.03.016>
- Perkins LB, Leger EA, Nowak RS (2011) Invasion triangle: an organizational framework for species invasion. *Ecol Evol* 1:610–625. <https://doi.org/10.1002/ece3.47>
- Pernilla Brinkman E, Van der Putten WH, Bakker E-J, Verhoeven KJF (2010) Plant-soil feedback: experimental approaches, statistical analyses and ecological interpretations. *J Ecol* 98:1063–1073. <https://doi.org/10.1111/j.1365-2745.2010.01695.x>
- Pokorny ML, Sheley RL, Zabinski CA et al (2005) Plant functional group diversity as a mechanism for invasion resistance. *Restor Ecol* 13:448–459. <https://doi.org/10.1111/j.1526-100X.2005.00056.x>
- Prati D, Bossdorf O (2004) Allelopathic inhibition of germination by *Alliaria petiolata* (Brassicaceae). *Am J Bot* 91:285–288. <https://doi.org/10.3732/ajb.91.2.285>
- Qin R-M, Zheng Y-L, Valiente-Banuet A et al (2013) The evolution of increased competitive ability, innate competitive advantages, and novel biochemical weapons act in concert for a tropical invader. *New Phytol* 197:979–988. <https://doi.org/10.1111/nph.12071>
- R Development Core Team (2014) R: A language and environment for statistical computing
- Ruckli R, Hesse K, Glauser G et al (2014a) Inhibitory potential of naphthoquinones leached from leaves and exuded from roots of the invasive plant *Impatiens glandulifera*. *J Chem Ecol* 40:371–378. <https://doi.org/10.1007/s10886-014-0421-5>
- Ruckli R, Rusterholz H-P, Baur B (2014b) Invasion of an annual exotic plant into deciduous forests suppresses arbuscular mycorrhiza symbiosis and reduces performance of sycamore maple saplings. *For Ecol Manage* 318:285–293
- Ruckli R, Rusterholz H-P, Baur B (2016) Disrupting ectomycorrhizal symbiosis: Indirect effects of an annual invasive plant on growth and survival of beech (*Fagus sylvatica*) saplings. *Perspect Plant Ecol Evol Syst* 19:12–20. <https://doi.org/10.1016/J.PPEES.2016.01.005>
- Rusterholz HP, Küng J, Baur B (2017) Experimental evidence for a delayed response of the above-ground vegetation and the seed bank to the invasion of an annual exotic plant in deciduous forests. *Basic Appl Ecol* 20:19–30. <https://doi.org/10.1016/j.baee.2017.02.004>
- Schenk HJ (2006) Root competition: beyond resource depletion. *J Ecol* 94:725–739. <https://doi.org/10.1111/j.1365-2745.2006.01124.x>
- Smith NS, Côté IM (2019) Multiple drivers of contrasting diversity: invasibility relationships at fine spatial grains. *Ecology* 100:e02573. <https://doi.org/10.1002/ecy.2573>
- Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. *Front Ecol Environ* 1:11–14. [https://doi.org/10.1890/1540-9295\(2003\)001%5b0011:TRGRPO%5d2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001%5b0011:TRGRPO%5d2.0.CO;2)
- Stohlgren TJ, Jarnevich C, Chong GW, Evangelista PH (2006) Scale and plant invasions: a theory of biotic acceptance. *Preslia* 78:405–426
- Taylor K (2009) Biological flora of the British Isles: *Urtica dioica* L. *J Ecol* 97:1436–1458. <https://doi.org/10.1111/j.1365-2745.2009.01575.x>
- Thomsen MA, D'Antonio CM (2007) Mechanisms of resistance to invasion in a California grassland: the roles of competitor identity, resource availability, and environmental gradients. *Oikos* 116:17–30
- Tickner DP, Angold PG, Gurnell AM et al (2001) Hydrology as an influence on invasion: experimental investigations into competition between the alien *Impatiens glandulifera* and the native *Urtica dioica* in the UK. In: Brundu H, Brock J, Camarda I et al (eds) *Plant invasions: species ecology and ecosystem management*. Backhuys Publishers, Leiden, pp 159–168
- van der Putten WH, Bardgett RD, Bever JD et al (2013) Plant-soil feedbacks: the past, the present and future challenges. *J Ecol* 101:265–276. <https://doi.org/10.1111/1365-2745.12054>
- Vilà M, Espinar JL, Hejda M et al (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Vitousek PM, D'Antonio CM, Loope LL et al (1997) Introduced species: a significant component of human-caused global change. *N Z J Ecol* 21:1–16
- Vivanco JM, Bais HP, Stermitz FR et al (2004) Biogeographical variation in community response to root allelochemistry: novel weapons and exotic invasion. *Ecol Lett* 7:285–292. <https://doi.org/10.1111/j.1461-0248.2004.00576.x>
- Wood CW, Reeves DW, Himelrick DG (1993) Relationships between chlorophyll meter readings and leaf chlorophyll concentration, N status, and crop yield: a review. *Proc Agron Soc N Z* 23:1–9
- Zeiter M, Stampfli A (2012) Positive diversity-invasibility relationship in species-rich semi-natural grassland at the neighbourhood scale. *Ann Bot* 110:1385–1393. <https://doi.org/10.1093/aob/mcs193>
- Zheng Y, Feng Y, Valiente-Banuet A et al (2015) Are invasive plants more competitive than native conspecifics? Patterns vary with competitors. *Sci Rep* 5:15622. <https://doi.org/10.1038/srep15622>

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