Received: 24 July 2017 | Accepted: 27 November 2017

DOI: 10.1111/1365-2745.12928

RESEARCH ARTICLE

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

Functional trait differences and trait plasticity mediate biotic resistance to potential plant invaders

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Funding information
ERA-Net BiodivERsA; DFG (German Research Foundation); ANR (French National Research Agency); FWF (Austrian Science Fund), Grant/Award Number: I-1443-B25; Roma Tre University

Handling Editor: Jane Catford

Abstract

1. Biotic resistance represents an important natural barrier to potential invaders throughout the world, yet the underlying mechanisms that drive such resistance are still debated. In theory, native communities should repel both functionally similar invaders which compete for the same resources, and invaders which possess less competitive traits. However, environmental stress, trade-offs across vital rates and competition-induced plastic trait shifts may modify expected competitive outcomes, thereby influencing invasion dynamics.
2. In order to test these theoretical links between trait distributions and biotic resistance, we performed a mesocosm experiment with 25 non-native ornamental species invading native plant communities. Each non-native species was grown with and without the native community under two watering treatments (regular and reduced). We measured biotic resistance as the difference in performance of non-native individuals grown with and without the community in terms of their survival, growth and reproduction. We quantified overall functional dissimilarity between non-native ornamental individuals and native communities based on the combination of plant height, specific leaf area and seed mass. Then, assuming each of these traits is also potentially linked to competitive ability, we measured the position of non-natives on trait hierarchies. While height is positively correlated with competitive ability for light interception, conservative leaf and seed characteristics provide greater tolerance to competition for other resources. Finally, we quantified plastic trait shifts of non-native individuals induced by competition.
3. Indeed, the native community repelled functionally similar individuals by lowering the invader's survival rate. Simultaneously, shorter ornamental individuals with larger specific leaf areas were less tolerant to biotic resistance from the community across vital rates, although the effect of trait hierarchies often depended on watering conditions. Finally, non-natives responded to competition by shifting their

traits. Most importantly, individuals with more competitive traits were able to overcome biotic resistance also through competition-induced plastic trait shifts.

4. *Synthesis*. Our results highlight that both functional dissimilarity and trait hierarchies mediate biotic resistance to ornamental plant invaders. Nevertheless, environmental stress as well as opposing trends across vital rates are also influential. Furthermore, plastic trait shifts can reinforce potential invaders' competitive superiority, determining a positive feedback.

KEYWORDS

competition, Darwin's naturalization hypothesis, drought, fitness differences, intraspecific trait variability, invasion ecology, mesocosm experiment, niche differences, stress, vital rates

1 | INTRODUCTION

Biological invasions are a major threat to biodiversity, often leading to a significant loss of ecosystem functions and services (Hulme, 2012; Simberloff et al., 2013). The global horticultural trade is the main pathway through which non-native plants have been introduced worldwide, making non-native ornamental species the largest and most diverse pool of potential new invaders in Europe (Lambdon et al., 2008). Biotic resistance from native communities is one key natural barrier for non-native ornamental species to become invasive (Richardson et al., 2000). However, the underlying mechanisms that drive such resistance are still unresolved (Gallien & Carboni, 2017; Levine, Adler, & Yelenik, 2004). Anticipating which introduced species may escape cultivation, naturalize, become invasive and ultimately threaten native diversity is crucial for biodiversity conservation, especially with globalization increasing the introduction of ornamental species into new areas. Therefore, understanding how biotic resistance by native communities might prevent new invasions is of primary importance.

A useful theoretical framework for studying biotic resistance to invasion is provided by the ecological filtering metaphor of community ecology (Weiher & Keddy, 1995), focused on functional traits and ecological similarity (Gallien & Carboni, 2017). In fact, negative biotic interactions deriving from resource competition have often been related to the ability of native communities to resist invasions and filter newcomers (Eskelinen & Harrison, 2014; Kempel, Chrobock, Fischer, Rohr, & van Kleunen, 2013; Levine et al., 2004). However, certain non-native species should tolerate biotic resistance better than others because they possess functional traits that allow them to cope with competition more efficiently. On the one hand, functional similarity which is indicated by similar trait values is often associated with similar resource use (i.e. similar niches). Therefore, functional/niche dissimilarity to the native community may allow non-native species to limit resource competition with the natives (symmetric niche-based competition; Thuiller et al., 2010). On the other hand, hierarchical differences in the competitive abilities or fitness differences of the species should generally favour particular competitors over others (Chesson, 2000; Kraft, Godoy, & Levine, 2015; MacDougall, Gilbert, & Levine, 2009). Therefore, for traits related to competitive ability (e.g. Grime, 2001), competitive outcomes between non-native species and the native community will depend on their respective positions on competitive ability hierarchies (hierarchical competition related to fitness differences, Mayfield & Levine, 2010; Goldberg & Landa, 1991). For example, a non-native species which is taller than the native community will be more competitive in terms of light acquisition, which can give the non-native an advantage in the invasion process. Furthermore, a non-native species with a more conservative resource acquisition strategy (e.g. lower specific leaf area [SLA], heavier seeds) is typically less suppressed by resource competition with its neighbours, making it potentially more tolerant to biotic resistance (Goldberg & Landa, 1991). Ultimately, both functional dissimilarity and trait hierarchies can influence the outcome of new ornamental invasions in native communities once the dispersal and climatic barriers are overcome (Gallien & Carboni, 2017; MacDougall et al., 2009).

The mode and importance of competitive interactions in regulating invasions critically depend on environmental conditions and might change for different vital rates (survival, growth and reproduction, Li et al., 2015). For example, competitive interactions are often weaker under stressful conditions (Bertness & Callaway, 1994), and plants are often considered particularly sensitive to abiotic conditions in the establishment phase, which largely depends on seedling survival (Donohue, Rubio de Casas, Burghardt, Kovach, & Willis, 2010), but they are more constrained by competition during their growth (Primack & Kang, 1989). Therefore, the role of trait differences in determining invasion outcomes is also likely to change depending on the environment as well as throughout the life cycle of the introduced species, as many observational studies (e.g. Gallien et al., 2015; MacDougall, Boucher, Turkington, & Bradfield, 2006) and experiments (e.g. De Roy et al., 2013; Li et al., 2015) suggest. Accounting for such context-dependence of competitive interactions and related trait differences is important to correctly assess potential biotic resistance to escaping non-native ornamental plants.

Finally, although trait plasticity is often thought to be a key element in biological invasions (Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006), most community invasion studies still use average species-level trait values to assess ecological similarities (e.g. Carboni et al., 2016). However, horticulture might be expected to select particularly plastic species in gardening, in order to provide greater drought tolerance,

for example (Kendal, Williams, & Williams, 2012). Recent studies have shown that considering trait values at the individual level (i.e. the intraspecific trait variability partially resulting from plasticity) can strengthen the link between trait differences and community-assembly mechanisms (Bennett, Riibak, Tamme, Lewis, & Pärtel, 2016; Kraft, Crutsinger, Forrestel, & Emery, 2014; Siefert et al., 2015). In addition to environmentally driven plasticity, changes in trait expression induced by competition can also affect competitive outcomes, suggesting that both trait hierarchies and functional dissimilarity ultimately depend on how traits respond to competitors (Turcotte & Levine, 2016). While competition-driven plastic responses of the natives are likely to be important mostly in determining the impacts of invasions at an advanced stage, trait shifts of the introduced species can define the outcome of the invasion process already at an early stage. In some cases, plasticity induced by competition from the natives might enhance invasion success of non-native ornamental species by allowing them to overcome biotic resistance (e.g. Schiffers, Tielbörger, Tietjen, & Jeltsch, 2011; Figure 1b). In other cases, plastic trait shifts might not lead to stronger competitiveness (e.g. Milberg, Karlsson, & Wessman, 2014), or might even reinforce resistance of the native community. For example, a "passive" trait shift of the invader caused by limited availability of resources (van Kleunen & Fischer, 2005) can result in greater fitness differences with the natives (Figure 1a). Whether and how invaders plastically respond to competition is likely to depend both on their position on the competitive hierarchy and on the overall strength of biotic resistance.

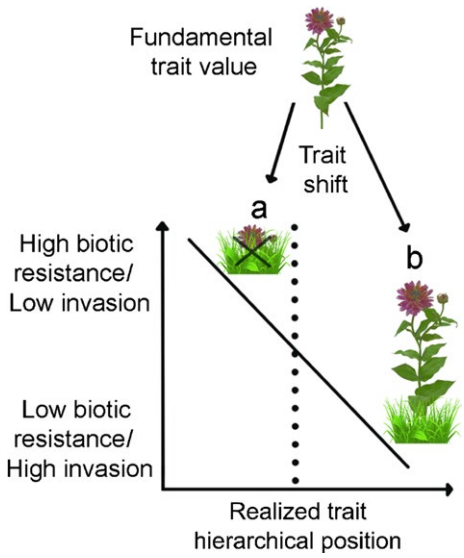

FIGURE 1 Trait shifts, biotic resistance and trait hierarchical position. A competition-induced trait shift is the difference between the fundamental-niche trait value (value measured without competition) and realized-niche trait value (which is the result of competitive interactions) of a given non-native ornamental species. In this example considering plant height, the realized value resulting from the trait shift can be lower (a) or higher (b) than the mean value of the native species in the community (dashed line). As plant height can mediate competitive outcomes, for example in relation to light interception (Westoby, 1998), shifts towards higher values can therefore result in the ornamental species being able to overcome biotic resistance and successfully invade (b), while non-adaptive shifts towards lower values will not (a). Figure inspired by and adapted from Turcotte and Levine (2016) [Colour figure can be viewed at wileyonlinelibrary.com]

Here we tested through a large mesocosm experiment and trait analyses when and how biotic resistance can prevent invasion of non-native plants, using 25 non-native ornamental species invading a native plant community. We considered the two modes by which trait differences reflect competitive interactions (functional dissimilarity and hierarchy), the context-dependence of competition and the possibility of competition-induced trait shifts. We specifically addressed three main questions: (1) How are functional dissimilarity and position on trait hierarchies of non-native ornamentals related to biotic resistance of the native community? (2) How do these relationships change under drought stress and across vital rates (survival, growth and reproduction)? (3) Does competition influence trait expression of non-native ornamentals and do competition-induced plastic trait shifts moderate their ability to overcome biotic resistance? Based on theory, we would expect that non-native ornamentals which are functionally distinct and more competitive on a trait hierarchy would experience less biotic resistance, but that the importance of this biotic filter would vary across vital rates in the course of the life cycle and would be generally lower under drought stress. Competition-induced trait shifts should provide an advantage for potential invaders when the shift is towards a more competitive value of the trait.

2 | MATERIALS AND METHODS

2.1 | Experimental design

We set up an experiment in which an assembled community of native European grassland species was artificially invaded by 25 non-native ornamental species. To determine the effects of competition and drought stress, each non-native ornamental species was grown with and without the native community, under two watering treatments (regular and reduced).

The experiment took place in an experimental garden at Tübingen University (Germany) and lasted for 4 months during the growing season. In April 2014, we filled six hundred 4-L pots with a 1:2 mixture of local sand and local soil. In half of the pots, we sowed a seed mixture of nine native European species—three grasses and six forbs—which are common in central European grasslands (Table 1). In order to obtain fairly similar native communities across all pots, seed mixtures contained exactly 5 seeds of each forb and 10 seeds of each grass (60 seeds in total). With this mixture, we aimed to reflect European grassland-dominated communities. Nearly all native species were found in all the pots (see Appendix S2, Figure S2a for details on the composition of these communities). The 25 non-native species used were herbaceous ornamental plants, either annual or perennial, commonly cultivated in European gardens. They are all alien to Europe and not naturalized there, but often naturalized outside of Europe (Table 1; see Dullinger et al., 2017; Haeuser, Dawson, & van Kleunen, 2017 for details on species selection criteria). At the same time that the natives were sown in the pots, non-native ornamentals were sown

TABLE 1 Non-native and native plant species used in the experiment. The table also shows the number of regions where they appear listed as "Naturalized" in the Global Naturalized Alien Flora database (GloNAF, van Kleunen et al., 2015; https://glonaf.org/)

Family	Name	Life span	Native region	Naturalized regions
Non-native ornamentals				
Amaranthaceae	*Amaranthus tricolor*	A	Tropical Asia	54
Boraginaceae	*Nemophila maculata*	A	SW USA	–
	Heliotropium arborescens	P	Peru	6
	Eritrichium canum	A	C Asia to Pakistan	–
Campanulaceae	*Platycodon grandiflorus*	P	NE Asia and Japan	5
Asteraceae	*Centaurea americana*	A	S and C USA, NE Mexico	–
	Helianthus debilis	A	E USA	5
	Zinnia peruviana	A	USA, Argentina and the West Indies	39
	Achillea filipendulina	P	Caucasus to C Asia	13
	Centaurea macrocephala	P	Turkey, Caucasus	11
	Helenium bigelovii	P	SW USA	9
	Rudbeckia fulgida	P	S and E USA	2
	Rudbeckia triloba	P	E USA	1
Lamiaceae	*Monarda fistulosa*	P	E and C Canada, USA, Mexico	1
	Monarda punctata	P	USA	1
	Nepeta racemosa	P	Caucasus, N and NW Iran	6
Plantaginaceae	*Digitalis trojana*	P	Turkey	–
Poaceae	*Pennisetum macrourum*	P	S Africa	15
Polemoniaceae	*Gilia tricolor*	A	SW USA	1
Polygonaceae	*Persicaria capitata*	P	Himalayan region	34
Solanaceae	*Nicotiana mutabilis*	A	S Brazil	–
	Petunia integrifolia	A	S Brazil, Paraguay, NW Argentina	16
	Salpiglossis sinuata	A	Andean Chile, Argentina	2
	Nicotiana sylvestris	P	Argentina	4
Verbenaceae	*Verbena rigida*	P	Argentina and S Brazil	54
Natives				
Asteraceae	*Achillea millefolium*	P	Temperate Northern Hemisphere	107
	Centaurea jaceae	P	Europe	53
	Leucanthemum ircutianum	P	Europe, Asia	–
Dipsacaceae	*Knautia arvensis*	P	Europe, W Asia	34
Lamiaceae	*Prunella vulgaris*	P	Europe, Asia, N America	119
Plantaginaceae	*Plantago lanceolata*	P	Europe	226
Poaceae	*Anthoxanthum odoratum*	P	Europe, Asia	119
	Arrhenatherum elatior	P	Europe, N Africa, W Asia	126
	Poa pratensis	P	Europa, Asia, N Africa, N America	182

A, annual; P, perennial.

in germination trays from seeds purchased from commercial suppliers. After 3–4 weeks, when natives and ornamentals had germinated and were of about equal size, a single seedling of each ornamental species was transplanted into the centre of each pot. For each non-native ornamental species, we grew 24 individuals: 12 replicates with a native community and 12 replicates grown individually without the community. To exclude precipitation, all pots were placed in the experimental garden under plastic greenhouses, with fully opened sides at eye level to prevent potential effects on temperature and/or evaporation. After some further establishment time (1–2 weeks), we randomly assigned half of the pots to one of two watering treatments: (1) a "regular" watering treatment where the plants were well watered (with 250 ml per pot) and did not experience any drought stress, and (2) a "reduced" watering treatment where the plants received only 50% of that amount of water (125 ml per pot), experiencing therefore a drought stress. Watering

was performed every day or every second day, depending on air temperature. Although watering in the reduced watering treatment was strongly diminished, we watered the plants frequently enough to prevent the plants from wilting completely. Within the greenhouse, the pots were arranged in 12 spatial blocks, each assigned to a different treatment and containing a random pair of pots of an ornamental species: one without competition, alone in the pot, and one with competition, with the native community.

In each pot, we quantified three vital rates or performance measures of the ornamental individual: survival (days of survival), growth (above-ground biomass) and reproduction (number of flowers). We recorded the survival of all ornamentals every week throughout the experiment. At the end of the experiment, in early September, we harvested, dried and weighed the above-ground biomass of all plants in each pot, separately for each species in both non-native ornamentals and natives. For the ornamental individuals, we also assessed the number of flowers produced at the end of the experiment, though we acknowledge that flowering is only a coarse proxy of reproduction effort or reproductive success. In a few pots there were spontaneous weeds that had not been sown, but as they were rare and small, we excluded them from further analyses. All 32 ornamental individuals that died in the first 2 weeks after transplanting were excluded from further analyses to account for transplant-related mortality.

2.2 | Biotic resistance

Biotic resistance to a potential invader is defined as the native community's competitive effect on the performance of the invader species. All other conditions being equal, greater biotic resistance towards a particular species will result in lower invasion success by that species within the community. Here we assessed variation in the strength of biotic resistance by comparing the *competitive response* of different target ornamental species to the same native community (sensu Goldberg & Landa, 1991). Good response competitors will experience low biotic resistance, whereas high biotic resistance indicates worse response competitors. Operationally, we quantified the strength of biotic resistance to each ornamental by calculating the percentage reduction in success in terms of survival, growth and reproduction of the non-native individual in the community pots compared to the average success of the individuals of the same species in the same treatment growing alone (Cahill, Kembel, Lamb, & Keddy, 2008):

$$\text{Biotic resistance} = \frac{\overline{\text{Success}}_{\text{alone}} - \text{Success}_{\text{withcommunity}}}{\overline{\text{Success}}_{\text{alone}}}$$

For biotic resistance to growth and reproduction, we only considered the community pots where the ornamental had survived until the end of the experiment. Because here we focus on competition, we did not account for potential facilitative effects of the community, and we treated the few observations where there was greater success in the presence of the native community (23/298 observations for survival and 2/268 observations for growth and reproduction) as no competitive effect of the native community (i.e. we set biotic resistance to zero).

2.3 | Trait selection and measurement

We searched for a relationship between the variation in biotic resistance towards different ornamentals and the variation in their functional traits. Specifically, we measured three synthetic functional traits that are considered to represent key axes of plant ecological strategies (Westoby, 1998): plant height, SLA and seed mass. Plant height is associated with competitive strength for light interception (Westoby, 1998). Specific leaf area is positively correlated with relative growth rate and reflects species differences in resource use strategies (for both water and nitrogen). While higher SLA values indicate investment in growth and rapid resource acquisition (exploitative strategy), lower SLA values indicate investment in leaf storage tissues and more conservative resource use (conservative strategy, Pérez-Harguindeguy et al., 2013). Finally, seed mass is a component of reproductive effort (Pérez-Harguindeguy et al., 2013), but in the context of our experiment it is mostly related to growth rate at the juvenile stage (small seeds tend to produce rapidly growing seedlings, Turnbull, Paul-Victor, Schmid, & Purves, 2008) and to seedling tolerance to harsh conditions (seedlings from larger seeds are more likely to survive under harsh conditions, Moles & Westoby, 2006). Together, these traits inform about the overlap between species in resource use strategy and about their relative competitive ability (in terms of competitive responses).

Shortly before harvesting, we measured the height (cm) and the SLA on one leaf (mm^2/mg) for all feasible ornamental individuals in the experiment. On a total of 553 surviving ornamental individuals, we measured height in 551 individuals and SLA on 520 individuals. For each native species and in each treatment, we measured SLA and height on 6 and 10 randomly chosen individuals respectively. As not all of the individuals in the experiment produced seeds, we used the supplier's seeds for all measurements to estimate seed mass (mg) of both ornamentals and natives. We performed one measurement per all 34 species in the experiment based on multiple seeds, depending on the size of the single seed (10 seeds per measurement in average). We followed the instructions of Pérez-Harguindeguy et al. (2013) for all measurements. All traits were standardized (by subtracting the mean and dividing by 1 *SD*) and their distribution normalized through log-transformation for further analyses. See Appendix S1 for details on the ornamental species' trait values and Appendix S2 for details on the native species' trait values.

For computing functional differences between ornamentals and natives, we generally used the traits *realized* in the pots, which account for plasticity. Specifically, for non-native ornamentals we used the specific trait value measured on the individuals in each community pot. In the pots where the ornamental did not survive, we used our best available approximation of its realized trait value, which was the mean value for that species in the same treatment combination. Note that this approximation was only needed when analysing biotic resistance to survival, as individuals that did not survive were not used to

analyse growth and reproduction. For the natives we used the average trait values of individuals measured in the appropriate treatment, by pooling separately pots within each treatment. Trait responses of natives to competition from the invader were assumed to be negligible, as we only transplanted one ornamental individual in the pot. For seed mass, we used only average values in all analyses, as this trait was only measured on supplier's seeds, i.e. never in the community pots.

For comparison, we also assessed functional differences based on *fundamental* trait values, which do not account for plasticity. To obtain *fundamental* traits, we averaged trait values at the species level by pooling pots across treatments. In the case of ornamentals, we used only individuals growing alone (i.e. without competition), assuming that this is close to representing the species' fundamental niche. Analyses using *fundamental* traits instead of *realized* traits led to qualitatively similar results, although models based on *fundamental* traits generally explained a considerably lower portion of variability (see Appendix S5). Therefore, in the following, we present results based on the *realized* traits, unless otherwise specified.

2.4 | Functional differences

For each community pot, we quantified functional differences between the ornamental and the community by measuring (1) the combined functional dissimilarity across all three traits (height, SLA and seed mass) and (2) the position of the ornamental on trait hierarchies, for each trait independently. For the multi-trait "functional dissimilarity" to native species, we used the Euclidean (absolute) distance in three dimensions calculated for the three traits, weighted by the biomass of each of the native species in the pot (Thuiller et al., 2010). This metric should capture potential for overall overlap in the use of resources. For the hierarchical single-trait metrics, we calculated the position of each ornamental on each trait hierarchy (Gallien et al., 2015) to obtain a measure of how much higher or lower the ornamental's trait value was in comparison to the (unweighted) average trait values of the co-occurring natives (trait hierarchical position = $\text{Trait}_{\text{ornamental}} - \overline{\text{Trait}}_{\text{natives}}$). Values are zero when the invader has the same trait value as the community average, and negative or positive when the invader has a lower or higher value than the community respectively. We assume that the position in the trait hierarchy quantifies the competitive ability difference between individuals relative to that specific trait (Goldberg & Landa, 1991; Kunstler et al., 2012). Specifically we expect: (1) taller species to be overall better competitors for light (e.g. Kunstler et al., 2012); (2) species with low SLA values associated with slow growth rates and a conservative strategy to be better response competitors (e.g. Kraft et al., 2014); and (3) species with larger seeds associated with slower seedling growth rates to be more tolerant to resource competition.

2.5 | Trait shifts

Finally, we quantified competition-induced trait shifts (or plasticity) of non-native species, i.e. the effect of the native community on the trait values of the non-native individuals by calculating the proportional change between plant height and SLA values of the ornamentals growing with the native community and the average trait values of the individuals of the same species in the same treatment growing alone:

$$\text{Trait shift} = \frac{\text{Trait value}_{\text{withcommunity}} - \overline{\text{Trait value}}_{\text{alone}}}{\overline{\text{Trait value}}_{\text{alone}}}$$

A positive trait shift means that the presence of the native community increases the ornamental's trait value, while a negative trait shift means the opposite. This shift does not necessarily need to be towards a more adaptive value of the trait (Sultan, 2000; van Kleunen & Fischer, 2005). Although we did not control for genetic identity of the plants, we refer to these trait shifts as "plastic response." As we had no realized trait values for seed mass, we could obtain trait shift values only for plant height and SLA. Note that competition-induced shifts in mass of the seeds produced by the ornamentals would not affect the competitive outcomes in the course of the experiment but only in the following generation, which is not analysed in this experiment. In total, we used 262 observations for height trait shift and 236 observations for SLA trait shift.

2.6 | Statistical analyses

We fitted linear mixed effect models (LMM; R package lme4, version 1.1-12; Bates, Mächler, Bolker, & Walker, 2015) to explain the strength of (1) biotic resistance and (2) trait shifts.

First, to test whether the strength of biotic resistance to different ornamental species was explained by the functional traits of the invader relative to the native community and/or by drought stress (watering treatment), we fit a separate model for each vital rate. Thus, we obtained three full models explaining biotic resistance to survival, growth and reproduction. All biotic resistance variables, which are expressed in terms of proportional reductions, were transformed through logit transformation in order to normalize model residuals. The fixed effects in these models were: the watering treatment, the centred and standardized functional difference metrics (functional dissimilarity and trait hierarchies), interactions between watering treatment and functional differences, and life span of the ornamental species (annual or perennial). Note that Pearson correlation among the functional difference metrics was low ($R < .4$).

Second, we fitted separate models to investigate how trait shifts of the invaders were linked to competition by the native community. We tested whether the observed trait shifts of the ornamentals (i.e. the plastic response to the community) could be explained by their functional differences to the natives for that trait as well as by the biotic resistance they experienced on both growth and reproduction. Note that in these models we used functional differences based on *fundamental* traits as explanatory variable, as this represents the potential trait values from which the ornamental species deviate in response to competition. Functional traits for dead ornamental individuals could not be measured, and therefore resistance to survival could not be included in the trait shift models.

In both sets of models, ornamental species identity was included as a random intercept effect, nested in family to account for phylogenetic autocorrelation (its variability is presented in Appendix S4, Figure S4a–c for biotic resistance models and Figure S4d and e for trait shift models). For each model, we plotted the fixed effects on the standard deviation scale and considered relationships important if the 95% confidence intervals did not overlap zero. To estimate the explained variance of the fixed and random effect variables in the models, we calculated conditional and marginal R^2 values (R package MuMIn, version 1.15.6; Barton, 2016). Conditional R^2 accounts for the variance explained by both fixed and random effects, whereas marginal R^2 accounts for the variance explained by fixed effects only (Nakagawa & Schielzeth, 2013).

3 | RESULTS

3.1 | Contrasting and congruent effects across vital rates

Biotic resistance affected separate vital rates of ornamentals differently across environmental and functional gradients. Drought increased the biotic resistance of the native community to the ornamentals' survival, but lowered resistance to their growth and reproduction (Figure 2). While the link between functional dissimilarity and biotic resistance depended on the vital rate analysed, trait hierarchies for height and SLA affected biotic resistance more consistently across vital rates for both survival and growth (Figure 2). Overall, R^2 values were comparatively similar across vital rates, with the random effects explaining a larger proportion of variability (particularly for reproduction), and fixed effects explaining a smaller proportion but still up to 33% of explained variability (See Appendix S3).

3.2 | Biotic resistance to invaders' survival

The model for survival revealed that ornamental individuals that were functionally dissimilar to the natives were more likely to tolerate competition and live longer in the community (Figure 3a). Concurrently, shorter ornamental individuals experienced greater biotic resistance compared to taller individuals, and consequently survived fewer days in the native community (Figure 3b). However, this effect depended on the watering treatment and was accentuated in the pots exposed to reduced watering, i.e. under drought stress (Figure 3b). Similarly, watering conditions affected the mild relationship between biotic resistance to survival and seed mass hierarchical position (interaction term, Figure 3c). Thereby having larger seeds compared to the community resulted in an overall null advantage in terms of days of survival (non-significant main effect, Figure 2). For this model, higher marginal R^2 (.19) compared to conditional R^2 (.59) indicates that the fixed effect variables accounted for a third of the total variance explained by the model.

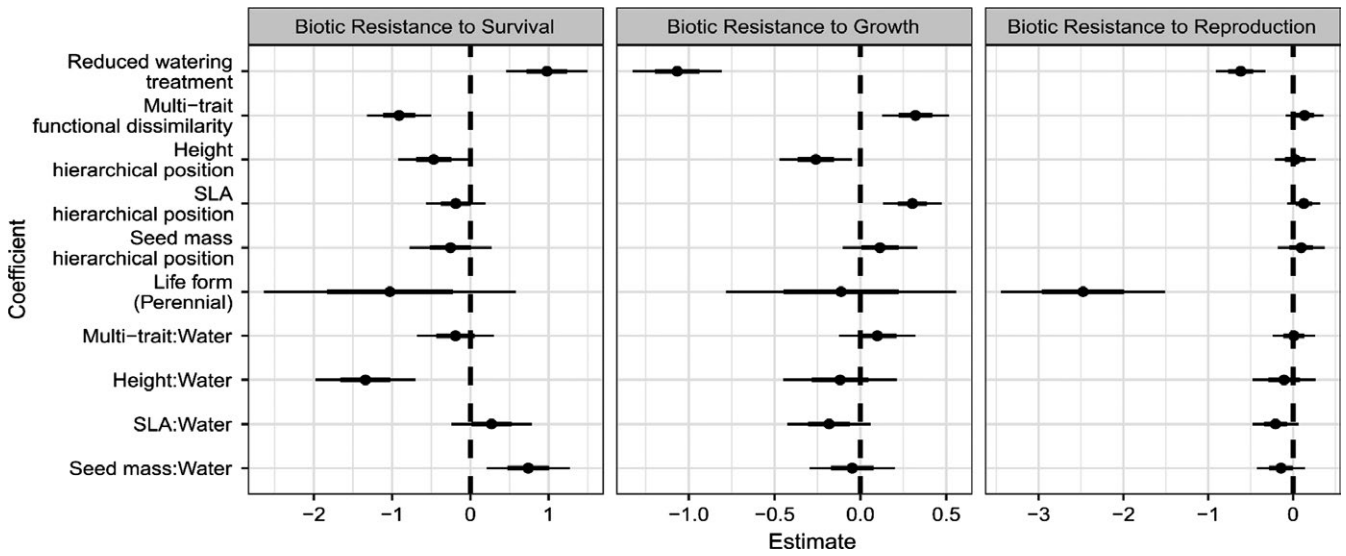

FIGURE 2 Effect sizes for fixed factors in the linear mixed effect models of biotic resistance to survival, growth and reproduction plotted on the standard deviation scale. Response variables indicate the native community's competitive effect on the performance of the invader species and were calculated as the percentage reduction in non-native individual's success in terms of survival, growth and reproduction in the community pots compared to the average success of same species' individuals in the same treatment growing alone. Models were fitted to the multi-trait functional dissimilarity, plant height hierarchical position, specific leaf area (SLA) hierarchical position and seed mass hierarchical position, and their interaction with the watering treatment. Trait metrics were calculated with the most accurate available trait values (i.e. realized for height and SLA and fundamental for seed mass). We consider effects important if the variables' 95% confidence intervals do not overlap zero. Dots show the effect estimates with thick lines indicating one standard deviation on either side (68% inner confidence intervals), and thin lines indicating two standard deviations (95% outer confidence intervals). The effect of the reduced watering treatment is shown in comparison to the regular watering treatment (reference level for this factor)

3.3 | Biotic resistance to invaders' growth

Contrary to our expectations, ornamentals that were functionally dissimilar to the natives were less able to tolerate biotic resistance in terms of their growth (Figure 3d). In terms of trait hierarchies, taller ornamentals and those with lower SLA values were better able to cope with biotic resistance and grow more (Figure 3e,f). For this vital rate, we found no significant interaction between the functional differences considered and the watering treatment. However, biotic resistance was generally lower under drought stress. Also for this model, marginal R^2 was relatively high (.30) compared to conditional R^2 (.78).

3.4 | Biotic resistance to invaders' reproduction

Besides drought (reduced watering treatment), which generally lowered biotic resistance, only life-form had a significant effect on the strength of biotic resistance to reproduction. Perennial individuals were more able to cope with competition compared to annual individuals across all treatments (Figures 2 and 3g). Marginal R^2 accounted for almost half the variability considered by the conditional R^2 (.35 and .87 respectively).

3.5 | Plastic trait shifts

The observed trait shifts in both plant height and SLA were explained partly by the natives' competitive effect on the ornamentals and partly by their position on the trait hierarchy (Figure 4). The watering treatment affected only SLA trait shifts, with greater shifts in the reduced watering treatment compared to the regular treatment (Figure 4).

Biotic resistance from the native community caused a general reduction in height for the ornamental individuals (Appendix S1, Figure S1a). Moreover, stronger competitive effects on growth of the community were associated with greater height reduction in ornamentals, as non-native individuals experiencing greater biotic resistance became smaller than expected based on their performance when grown alone (Figure 5a). The R^2 values indicate that a major portion of the variability of height trait shift was explained by the fixed effect variables alone (marginal R^2 = .53, while conditional R^2 = .74).

In the case of SLA, individuals grown in the community tended to shift towards higher SLA values compared to individuals grown alone (Appendix S1, Figure S1b). When biotic resistance to the ornamentals' growth was strongest, ornamental individuals shifted more in their SLA values (Figure 5b). Moreover, individuals of ornamental species with fundamentally higher SLA than the natives went through greater plastic trait shifts, producing leaves with even higher SLA (Figure 5c). However, as seen previously, having higher SLA values compared to the natives was associated with lower ability to cope with native's biotic resistance to growth (Figure 3e). Thus, shifts towards higher SLA values further lowered the ornamentals' ability to cope with biotic resistance, whereas shifts towards lower values reinforced the ornamentals' ability to cope with biotic resistance for those better competitors with fundamentally low SLA. The R^2 values indicate that most explained variability of SLA trait shifts depended on the fixed effect variables alone, but a considerable proportion of the overall variability was not explained by the variables in the model (marginal R^2 = .23, while conditional R^2 = .29).

4 | DISCUSSION

4.1 | How are trait differences between ornamentals and native communities related to biotic resistance?

Both multi-trait functional dissimilarity and trait hierarchies helped predict competitive outcomes, suggesting that both niche-based and hierarchical competition can influence the biotic resistance of native communities and ultimately curb future invasions by non-native ornamental plants. Teasing apart niche differentiation and fitness-related competition through traditional trait-based community metrics was considered difficult (Mayfield & Levine, 2010). However, recent studies showed that using hierarchical trait measures can help discern these two processes (e.g. Kraft et al., 2015; Kunstler et al., 2012). Specifically, by using field parameterized mathematical models of competition, Kraft et al. (2015) found significant relationships between trait hierarchies and competitive dominance as well as between multi-trait functional dissimilarity and stabilizing niche differences. Our results corroborate these findings, highlighting the usefulness of the functional approach to understand the mechanisms by which native communities repel potential invaders.

We found that metrics based on trait hierarchies provided consistent results across most vital rates, which were robust even when not accounting for intraspecific trait variability (see Appendix S5) and suggest a strong role for hierarchical competition in shaping biotic resistance to ornamental species. Specifically, taller ornamental individuals were predictably better at tolerating biotic resistance and were thus more successful in surviving and growing in communities, in agreement with theoretical predictions and empirical studies (Kraft et al., 2015; Mayfield & Levine, 2010). Furthermore, ornamental individuals with lower SLA, which are more conservative in their use of resources, could generally better endure competition from the natives, growing more than other individuals. Though SLA is sometimes considered to be positively correlated with competitive ability (Westoby, 1998), our result is in accord with previous studies linking better competitive responses (rather than competitive effects) to low SLA and relative growth rates (Goldberg & Landa, 1991; Kraft et al., 2014).

In addition, functionally distinct ornamentals underwent less mortality due to biotic resistance, in agreement with the resource opportunity hypothesis (or "Darwin's naturalization hypothesis," Thuiller et al., 2010). The results regarding survival are evidence of the role of limiting similarity and niche differentiation in filtering successful ornamental species especially in the establishment stage (MacDougall et al., 2009). Note that, once the ornamentals were established, biotic resistance to growth was actually lower for individuals that shared similar traits with the natives, but this was a consequence of the hierarchical effect of plant height (Figure 3e). Within the community, ornamental individuals tended to be generally shorter than the natives because of the reduction in their height induced by competition (Figure S1a in Appendix S1, and negative trait shift in Figure 5a).

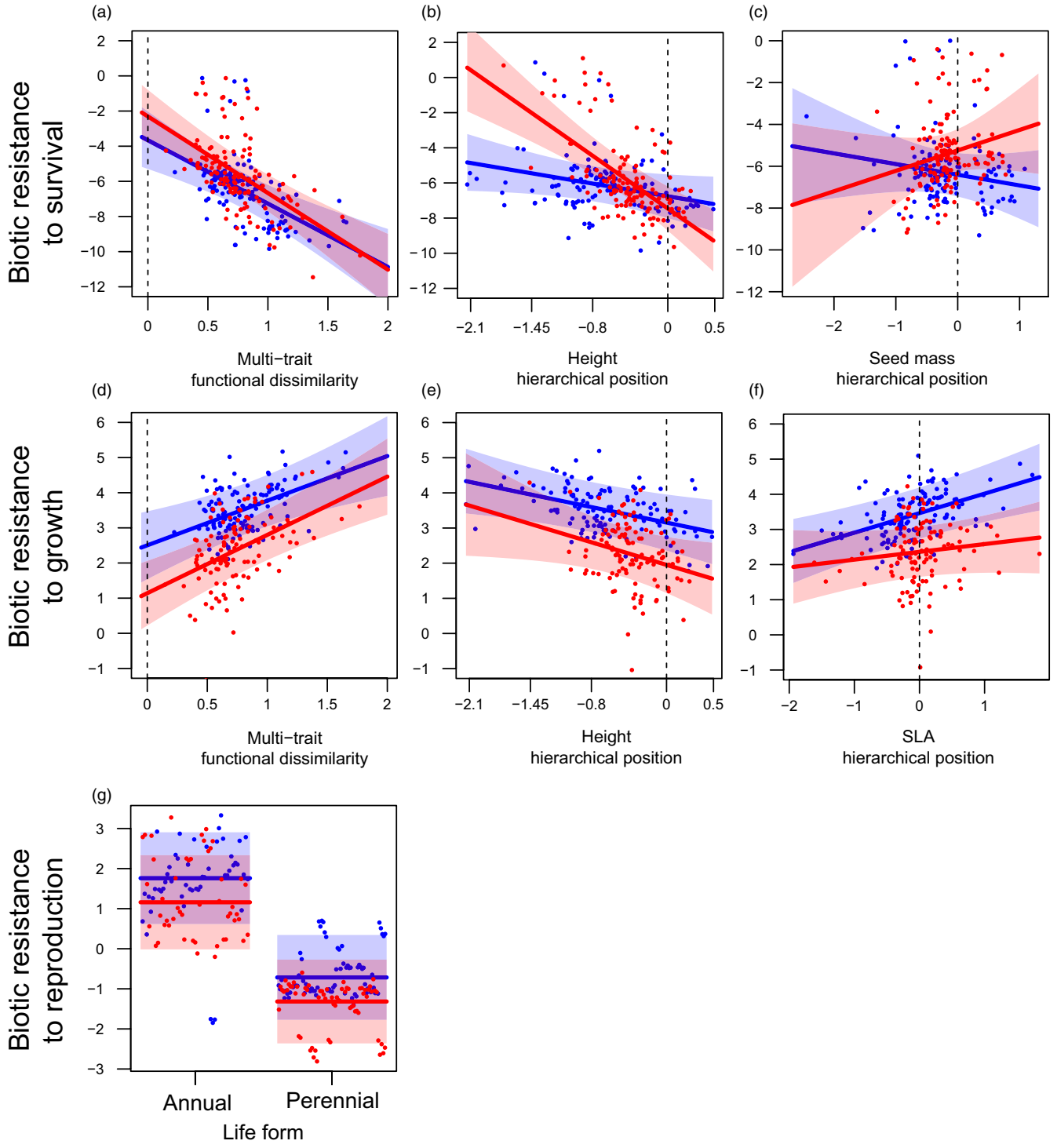

FIGURE 3 Partial residual plots of the principal fixed effects on the biotic resistance to survival (a, b, c), growth (d, e, f) and reproduction (g) of the invader (logit-transformed percentage reduction in non-native individual's success in the community pots compared to the average success of same species' individuals in the same treatment growing alone). Relationships for the regular and reduced watering treatment are represented in blue and red respectively (please refer to the online version of this article for colour coding). Regression lines are fitted for each of the treatments, shaded areas represent their 95% confidence intervals. Continuous explanatory variables are back-transformed for ease of interpretation. In panel g, lines indicate the mean value for each treatment and the points show the data variability (randomly jittered in each of the two treatments in the x-axis to avoid overlap) [Colour figure can be viewed at wileyonlinelibrary.com]

As a consequence, ornamental individuals that were most functionally similar to the natives were also the tallest, subject to low biotic resistance.

Overall we conclude that ornamental annuals that are taller and have a more conservative resource acquisition strategy but are also functionally distinct to a certain degree, are generally better at coping

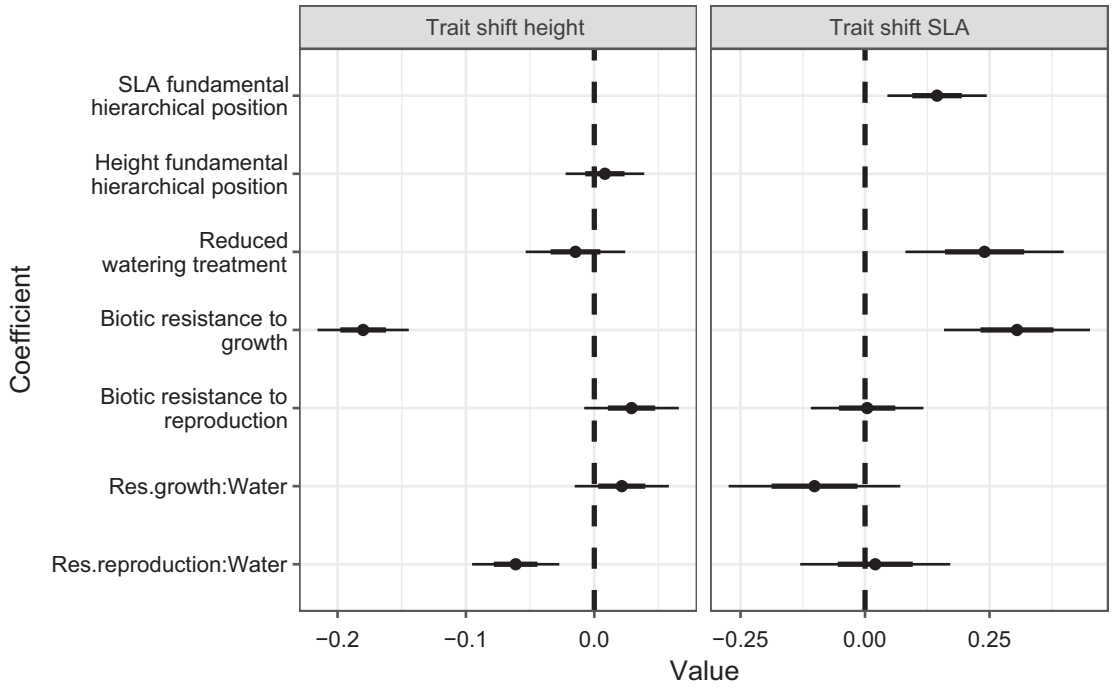

FIGURE 4 Fixed effects for the linear mixed effects models of plastic trait shifts for plant height and specific leaf area (SLA) plotted on the standard deviation scale. Response variables indicate the effect of the native community on the trait values of the non-native individuals and were calculated as the proportional change between plant height and SLA values of the ornamentals growing with the native community and the average trait values of the individuals of the same species in the same treatment growing alone. Models were fitted to the fundamental trait hierarchy of each trait considered (i.e. height hierarchy for trait shift in height, SLA hierarchy for trait shift in SLA), the community resistance to the ornamental's growth and reproduction and the interaction of community resistance with the watering treatment. We consider effects important if the variables' 95% confidence intervals do not overlap zero. Dots show the effect estimates with thick lines showing one standard deviation either side (68% inner confidence intervals), and thin lines indicating two standard deviations (95% outer confidence intervals)

with biotic resistance in central European grassland communities, and are therefore more likely to invade these communities. However, these trait-mediated biotic resistance mechanisms can change under drought stress and across vital rates.

4.2 | How does biotic resistance change under drought stress and across vital rates?

First, we found that the overall *strength* of biotic resistance on the vital rates of the ornamentals depended on drought stress (main effect of watering treatment). According to the well-known stress gradient hypothesis, we expected competition from the community to be weaker in stressful conditions (Bertness & Callaway, 1994). We did find support for this expectation, but only in terms of competitive suppression of growth and reproduction of the ornamental species in the native community. In contrast, the negative impact of the native community on the ornamentals' survival was stronger under drought, highlighting that different processes operate on specific vital rates.

Second, the *mode* of biotic resistance also depended on the vital rate (main effects of functional difference metrics). Patterns were consistent with niche-based competition for survival but more complex in terms of growth and reproduction (e.g. Li et al., 2015). While it is often suggested that seedling survival is mainly affected by local environmental conditions (Donohue et al., 2010) and less by competition, in our experiment the ornamentals' survival did decrease when exposed to drought stress, but was also affected by the surrounding native community, which suppressed the survival of functionally similar ornamental individuals (see also Kempel et al., 2013). By contrast, growth and reproductive success have often been linked to competition intensity (Primack & Kang, 1989), as these fitness components directly depend on the resources the individuals can effectively take up. In our experiment, however, functionally similar species encountered less competition from the natives in terms of biomass production. These apparently counterintuitive results actually fit well in MacDougall et al.'s (2009) framework linking plant invasions with dissimilarity. These authors suggested that niche differences should facilitate the establishment of invaders, not their dominance or impact in the community (Ricciardi & Cohen, 2007). Conversely, trait differences that increase the invaders' fitness in comparison to the natives should drive both establishment and competitive dominance and thus lead also to higher total biomass of invaders in communities. This pattern is congruent with our results linking trait hierarchies with multiple vital rates of ornamentals as well as niche-based competition with survival only.

Trade-offs between fitness components are known to occur during invasions (Richardson & Pyšek, 2006) with establishment, proliferation and propagation of non-native species depending on

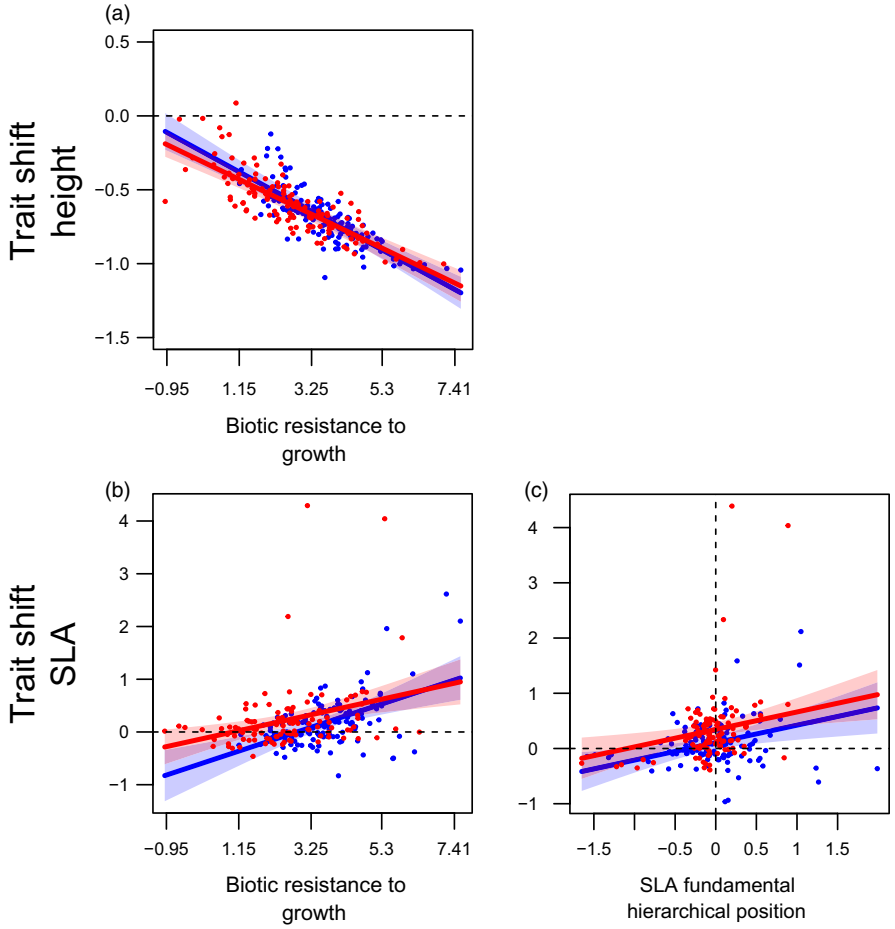

FIGURE 5 Partial residual plots of the principal fixed effects on the trait shift of height (a) and specific leaf area (SLA) (b, c) of ornamental plants. Relationships for the regular and reduced watering treatment are represented in blue and red respectively (please refer to the online version of this article for colour coding). Regression lines are fitted for each of the treatments, shaded areas represent their 95% confidence intervals. Explanatory variables are back-transformed for ease of interpretation. Horizontal dashed lines indicate no trait shift. The vertical dashed line on the 0-value in c indicates where the ornamental species has the same SLA as the native community [Colour figure can be viewed at wileyonlinelibrary.com]

different processes. In fact, opposing trends in vital rates across environments commonly occur in many plant populations ("demographic compensation," Villellas, Doak, García, & Morris, 2015). Nevertheless, how functional similarity with the native community affects the performance of invaders has rarely been tested experimentally on separate vital rates (but see Jiang, Tan, & Pu, 2010 and Li et al., 2015). Here, we found patterns indicating possible trade-offs, with few functionally similar ornamental individuals surviving to biotic resistance, but successively being able to tolerate the natives by growing and reproducing more (MacDougall et al., 2009).

Finally, the *mode* of biotic resistance was also partially dependent on watering conditions (interaction terms). For example, the competitive advantage of being taller for ornamental survival was stronger under drought, potentially because biotic resistance was a stronger filter for the survival of ornamentals in this treatment. By contrast, the expected negative relationship of biotic resistance with seed mass seemed to be reversed under drought: smaller seeds were more advantageous, even though larger seeds are also supposed to provide greater tolerance to harsh conditions (Moles & Westoby, 2006). However, note that ornamental species had generally smaller seeds than the natives, suggesting that limiting similarity might be driving this result (as emphasized by the greater importance of niche differentiation on survival rates). Although this result is controversial, it highlights the importance of environmental conditions for regulating the mode of biotic resistance in native communities.

As a caveat, we note that we only focused on survival, growth and reproduction of seedlings transplanted into newly established native communities, which means that we did not address how biotic resistance might affect germination of introduced species across environmental gradients. For example, traits related to early establishment success (such as seed mass) are likely to influence mechanisms of biotic resistance more in the germination phase, modulated by environmental disturbances (Kempel et al., 2013). This might also be why we found overall limited effects of seed mass in our experiment. However, differences in the germination stage can significantly alter invasion dynamics. Future studies should therefore examine biotic resistance mechanisms across more vital rates and additional gradients (e.g. disturbance and temperature). Furthermore, the considerable proportion of the variability that was not captured by the fixed effects in our models suggests that additional species characteristics (e.g. related to below-ground traits and to allocation to roots) are also likely to play a role. A final caveat concerns the short time frame of our study. Given the presence of perennial species in the experiment, the effect of biotic resistance on vital rates might vary in subsequent growing seasons. In particular, we could have overestimated biotic resistance to reproduction of the perennials, given that flowering might be postponed to the second year under unfavourably stressful or competitive

conditions. Here we accounted for this potential bias by including life-form in our modelling framework, yet longer multi-season studies are needed to fully assess this effect.

4.3 | Do competition-induced plastic trait shifts enhance non-native performance?

Trait plasticity is an important component of intraspecific trait variability, and ignoring it can impair the explanatory power of trait-based community analyses (Siefert et al., 2015). In this experiment, we confirm that disregarding intraspecific trait variability would lead to underestimating the links between functional differences and biotic resistance (Figure S4a), therefore making it more challenging to anticipate which non-native species can successfully establish based on its traits. Competition-induced trait plasticity has also been recently shown to play an important role for competitive outcomes within established communities (Bennett et al., 2016). Our results emphasize that trait plasticity also influences biotic resistance of newly established communities to newcomers, such as invasive ornamental species.

Specifically, our results suggest that trait plasticity of ornamental individuals determines a positive feedback of the competitive mechanisms in the invaded native community. We observed shifts in the height and SLA of ornamental individuals, although not necessarily towards a more competitive trait value. First of all, individuals exposed to stronger biotic resistance from the native community became predictably shorter, which further weakened their ability to compete for light and water uptake, as the trait shift verged towards a less adaptive value of the trait (Angadi & Entz, 2002). Thus, the shift in height towards less competitive trait values induced a positive feedback reinforcing biotic resistance towards short ornamental individuals. However, the lack of an effect of the height hierarchy calculated on fundamental trait values suggests that this shift is likely independent from the potential competitive ability for light of the invader.

Second, ornamental individuals growing in a competitive environment also shifted in their SLAs, potentially to cope with a more shaded environment at the expense of maximizing photosynthesis in direct light. However, ornamentals with fundamentally lower or similar values of SLA compared to the natives shifted even to lower SLA values when grown in the community, while individuals with fundamentally higher values of SLA produced even broader and thinner leaves. Because biotic resistance mostly affected the performance of individuals with high SLA values, ornamentals that invested in fast growth and resource acquisition were not efficient and became even worse competitors because of passive trait shifts, whereas more efficient species were additionally favoured because of competition-induced trait plasticity.

Generally, both these processes suggest a positive feedback to the trends found for the results linking trait dissimilarity and hierarchies with biotic resistance. Hence, our results suggest that plasticity is likely to influence native communities' ability to repel potential invaders and most importantly, it might reinforce the ability of the most competitive ornamentals to overcome biotic resistance irrespective of environmental conditions. These results align well with recent theoretical work suggesting that intraspecific variation in competitive ability should increase the dominance of superior competitors (Hart, Schreiber, Levine, & Coulson, 2016). Ours is the first experimental study demonstrating this link in the context of plant invasions.

5 | CONCLUSIONS

Our results support the growing evidence of a link between functional similarity and niche similarity, as well as between trait hierarchies and differences in competitive ability (i.e. fitness differences). Both were related to invasion dynamics of non-native ornamentals, but their effect depended on the vital rate analysed and on the drought stress level experienced by the community. Overall, we showed that community resistance to potential ornamental invasions is shaped by both niche-based and hierarchical competition mechanisms. Functionally distinct ornamental herbs, which are taller and have smaller and denser leaves geared to conserve water, are likely to better tolerate biotic resistance of central European native grassland communities and therefore might have a better chance to succeed in the invasion process. However, our findings suggest that the level of environmental stress, in particular drought stress, can affect the intensity and mode of biotic resistance in these native communities, potentially reducing its strength towards growth and reproduction of escaped ornamental species. Trade-offs and demographic compensation processes may also lead to greater invasiveness (i.e. expansion due to fast growth and reproduction) of ornamental plants in native communities. Finally, we showed that ignoring plastic responses to competition might lead to overlooking an important mechanism by which those ornamental species which are already most competitive tolerate biotic resistance, making them even more worrisome. Even though our results are based on a selection of European grassland species under relatively artificial conditions in mesocosms, functional differences, environmental stress, vital rates and competition-induced trait plasticity are likely to play an important role for biotic resistance across other types of native communities. Future experimental and field studies aimed at unravelling the mechanisms of biotic resistance to the next generation of plant invaders across habitats should not neglect the plastic response of non-native species to competition as well as changing competitive outcomes under different stress levels.

ACKNOWLEDGEMENTS

We thank F. Romiti for his help with the figures, I. Conti for revising the English language, as well as three anonymous reviewers and associate editor Jane Catford for their valuable comments on this manuscript. This research was funded by the ERA-Net BiodivERsA, with the national funders DFG (German Research Foundation), ANR (French National Research Agency), and FWF (Austrian Science Fund) (I-1443-B25), as part of the 2012-2013 BiodivERsA call for research proposals. L.C. was supported by Roma Tre University doctorate research funding program.

AUTHORS' CONTRIBUTIONS

M.C. conceived the study while attending a meeting with S.B., M.P., T.M., W.T., M.v.K., S.D., F.E., I.D., D.M., G.K. and O.B.; M.v.K. selected the ornamental species; S.B., M.P. and O.B. designed the mesocosm experiment; L.C. and S.B. conducted the experiment; L.C. analysed the data and wrote the first draft of the manuscript. All authors contributed substantially to improve analyses and manuscript.

DATA ACCESSIBILITY

The data supporting the results are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.n8v4m (Conti et al., 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Conti L, Block S, Parepa M, et al. Functional trait differences and trait plasticity mediate biotic resistance to potential plant invaders. *J Ecol*. 2018;106:1607–1620. https://doi.org/10.1111/1365-2745.12928