

# Impacts of dominant plant species on trait composition of communities: comparison between the native and invaded ranges

MARTIN HEJDA,<sup>1</sup> KATEŘINA ŠTAJEROVÁ <sup>1,2</sup>, JAN PERGL <sup>1</sup> AND PETR PYŠEK <sup>1,2,†</sup>

<sup>1</sup>Department of Invasion Ecology, Institute of Botany, The Czech Academy of Sciences, Průhonice CZ-252 43 Czech Republic

<sup>2</sup>Department of Ecology, Faculty of Science, Charles University, Viničná 7, Prague CZ-128 44 Czech Republic

**Citation:** Hejda, M., K. Štajerová, J. Pergl, and P. Pyšek. 2019. Impacts of dominant plant species on trait composition of communities: comparison between the native and invaded ranges. *Ecosphere* 10(10):e02880. 10.1002/ecs2.2880

**Abstract.** Most studies on the impacts of plant invasions focus on species richness or diversity of invaded communities, but much less attention has been paid to structural changes such as the representation of species with different traits. To bridge this knowledge gap, we assess the impact of dominant species on the trait composition of recipient communities (i.e., how species with certain height, seed mass, specific leaf area, clonality, and life form are represented in the vegetation plots sampled). We sampled vegetation that comprised three species native to Eurasia and invasive in North America (i.e., *Agrostis capillaris*, *Bromus tectorum*, and *Cirsium arvense*) and three species native to North America and invasive in Europe (i.e., *Aster novi-belgii*, *Lupinus polyphyllus*, and *Solidago canadensis*), in both their native and invaded ranges. This study system based on reciprocal inter-continental invasions allowed us to assess whether the impact on trait composition differed (1) between the native and invaded ranges and (2) between the two continents. The relationships between species' dominance and trait composition were tested using linear mixed-effect models and ordination methods. A general trend was that dominant species with an impact on species richness also had an impact on trait composition, especially in North America, where even the native dominants affected the trait composition of the community. Further, the impact of Eurasian dominants in North America was stronger than that associated with the opposite direction of invasion, due to a strong negative effect of Eurasian invaders on local tall clonal perennials. Our results show that (1) the traits of species in the invaded community co-determine the impact of invasion and are related to the impacts on species richness and composition; (2) the impacts on trait composition differ between the native and invaded ranges; and (3) the direction of invasion affects the impact on trait composition.

**Key words:** direction of invasion; Europe; impact; invaded range; invasive species; native dominant species; native range; North America; species traits.

**Received** 10 April 2019; revised 15 July 2019; accepted 18 July 2019; final version received 26 August 2019.

Corresponding Editor: Theresa M. Crimmins.

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† **E-mail:** petr.pysek@ibot.cas.cz

## INTRODUCTION

It is well-documented that invasive alien plants that achieve dominance in their invaded ranges affect various characteristics of resident plant communities, such as reducing the species' richness and diversity and changing the species composition (Hejda et al. 2009, Vilà et al. 2011, Pyšek et al. 2012). However, data documenting

whether this reduction in species richness and diversity is related to ecological traits of native species are still scarce (but see Hejda 2013b, Bravo-Monasterio et al. 2016, Smith et al. 2016, Divíšek et al. 2018).

It can be presumed that certain traits predispose resident species to being outcompeted by dominant aliens and, on the contrary, other traits enable species to coexist with invasive aliens. It

has been suggested that it is not the absolute values of the traits of native species that matter, but rather the relative distances in trait values between native and invasive species (see, e.g., Hejda et al. 2009, Brym et al. 2011, Hejda 2013b, Hejda and de Bello 2013, te Beest et al. 2015, Funk et al. 2016, Lee et al. 2016, Flinn et al. 2017). However, species can be also eliminated from the invaded community randomly, regardless of their ecological characteristics, or due to an unpredictable event, such as specific disturbance regimes.

The biogeography of plant invasions also affects their community-level impacts (Hierro et al. 2005, Hejda 2013a, Hejda et al. 2017), and many invasive species also suppress species' richness and diversity in their native ranges (Callaway et al. 2012, Ledger et al. 2015). Such community-level impacts of native dominants can be comparable to those of invasive species (Hejda et al. 2017). The direction of invasion, determined by the geographic location of the native as well as invaded ranges, can also affect the impact of invasion. A detailed example is available from a study comparing the impacts of one species across multiple invaded continents—the North American native species *Lupinus polyphyllus* has stronger negative impacts on the flora in New Zealand than in Europe (Hejda 2013a). This suggests that native species in central Europe are better adapted to coexist with this robust invasive species, than the native species in New Zealand. This is also consistent with the general pattern of stronger impacts associated with invasive species on islands compared to mainland (Pyšek et al. 2012). In addition, Eurasian species were shown to have more profound effects on native species richness in North America, than native North American species invasive in Europe (Hejda et al. 2017). For example, it is assumed that the invasion of European plants to temperate grasslands globally has been facilitated by their simultaneous introduction with pastoralism and cultivation, to which they were preadapted during millennia under human influences (di Castri 1989, MacDougall et al. 2018). Similarly, European archeophytes (i.e., species introduced before the end of Medieval; e.g., Pyšek et al. 2012) were more likely to become noxious weeds in North America and cause significant impacts on richness. This is a

consequence of extra-regional residence time which allowed for the selection of species or the evolution of traits that favored the colonization of arable habitats, and these are widespread, resource-rich, and uniformly distributed across the United States (La Sorte and Pyšek 2009).

In this study, we explore different aspects of community-level impacts of six dominant species: three native to Eurasia and invasive in North America and three native to North America and invasive in Europe. We examine the following questions: (1) What is the impact of dominant species on the composition of species traits of the resident community? This aim is based on the following rationale: if an invasive species reduces the richness of native species, but the degree of its dominance is not related to the changes in trait composition of the invaded community (i.e., a characteristic reflecting how species with certain height, seed mass, specific leaf area, clonality, and life form are represented in the vegetation plots sampled), it can be assumed that native species are eliminated at random. In contrast, if changes in trait composition are related to the degree of invasive species' dominance, native species with different traits also differ in their ability to coexist with the dominant invader. Moreover, the reciprocal design of this natural experiment allowed us to extend the rationale of the study with additional questions: (2) Do the impacts of dominant alien species on trait composition differ between the native and invaded ranges?, and (3) are there differences in species impacts between the two directions (i.e., species invading from Eurasia to North America and from North America to Europe)?

## MATERIALS AND METHODS

### *Species selection and sampling design*

We selected three species that are native to Eurasia and invasive in North America (i.e., *Agrostis capillaris*, *Bromus tectorum*, and *Cirsium arvense*) and three species native to North America and invasive in Europe (i.e., *Aster novi-belgii*, *Lupinus polyphyllus*, and *Solidago canadensis*; see Appendix S1: Table S1). We aimed to select species that (1) are strong dominants of plant communities in both the native and invaded ranges, and (2) occur in similar habitat types in both ranges (further termed as “target dominant

species”). These criteria were given priority because they were crucial for testing the questions formulated above. However, their application made it impossible to select dominant species with the same life forms and similar traits because the pool of strong dominant species in both the native and invaded ranges is rather restricted (see Hejda et al. 2017).

Furthermore, the taxonomic delimitation of the target species was not always consistent; therefore, we could not adopt a narrow taxonomic approach. For example, *Lupinus polyphyllus* in its native range of North America very likely includes some closely related species, such as *Lupinus burkei*. This situation might be further complicated in the invaded ranges as a result of hybridization for ornamental purposes and subsequent escape of such hybrids from cultivation. Similarly, the complex *Aster novi-belgii* agg. in the European invaded range includes *Aster novi-belgii* sensu stricto, but probably also *Aster lanceolatus* as well as newly established sterile hybrids that are not known from the native range. In the same way, the aggregate *Solidago canadensis* in Europe may also include very similar species of North American origin, such as *S. rugosa* (Landolt 2006), *S. altissima* (Szymura and Szymura 2015), or their hybrids, with invasive *Solidago gigantea* (Slavík and Štěpánková 2004, Nagy et al. 2017) or native *Solidago virgaurea* (Mlíkovský and Stýblo 2006). Consequently, from a strictly taxonomic perspective, we were dealing with taxa at the level of species aggregates. However, it can be assumed that the functional role of these taxa in plant communities would be largely similar, given the subtle ecological differences, and so their impacts are comparable between continents.

In North America and in Europe, we sampled the vegetation using the same methodology in order to yield a comparable dataset of the dominant species’ native and invaded ranges, as well as for species invading in both directions—from Europe to North America and vice versa. In both ranges (corresponding to the two continents), we sampled 40 plots 2 × 2 m in size, with varying degree of dominance (ranging from 10% to almost 100% of cover) of each of the target species. The small scale for individual plots was chosen on purpose, as we were primarily interested in the ability of species to grow within the relatively homogeneous stands of the target

dominants, rather than in the ability of species to grow in microsite-level gaps within the stands on the dominant species. In total, we sampled 480 vegetation plots—two continents × three invasive and three native dominant species on each continent × 40 replicates for each species on each continent. The plots were spatially clustered, as we sampled several plots within each suitable population of the target dominant species. The population was considered suitable, if it was large and heterogeneous enough so it was possible to locate plots with both large and low cover of the target dominant in it. This arrangement made sure that the plots with high versus low cover of the target dominant were compared within a single, homogeneous spatial unit, by adjusting the population’s identity as a random grouping variable within the LME models. Of course, the populations differed in their size and therefore also in the number of plots located in each—see Hejda et al. (2017) for more details on the sampling methods. In each plot, the percentage cover of all species (including the target dominant) was estimated. It was impossible to avoid the marginal presence of other alien species besides the target dominants in the plots, especially in North America. Plots were purposely selected to comprise only one dominant target species while the presence of other alien species was low enough so that they could not significantly impact the community-weighted mean (CWM) values (see Hejda et al. 2017 for more details on the sampling procedure, and Appendix S2: Table S1 for the description of the sampling sites).

Given the extent of the data and the requirement that a single researcher samples on both continents, it was not possible to account for different phenological aspects of the sampled communities. Rather, the communities on both continents were sampled in July and August 2011–2014, when the vegetation was fully developed and no further shifts in either species richness or composition could have been expected. Of course, it is possible that some of the early season species could have been missed but it was not the purpose of the study. However, the field experience showed that many of the spring species were still present even in the communities that were dry at the time of sampling, although these species were often in a state that they were difficult to determine properly. On the contrary,

the late summer was the perfect time for sampling in the tall grass prairies of USA, as many species of this vegetation type bloom in August.

In general, it was not possible to sample repeatedly for logistic reasons and, at the same time, it was not possible to design a single sampling time, which would be suitable for all types of the vegetation sampled. Rather, the time of sampling was a compromise between the phenological characteristics of different types of sampled communities. Most importantly, the plots with low versus high dominance of the target invaders were compared within the individual populations that were sampled during a single day. Therefore, a bias due to, for example, low-invaded plots being sampled earlier compared to high-invaded plots is extremely unlikely.

### Statistical analyses

*Expressing the representation of species with different traits using the community-weighted means method.*—The trait composition expresses the representation of species' ecological traits in individual vegetation plots using the community weighted mean (CWM) method (see Lepš and Šmilauer 2014). During this process, the values of species' traits are weighted by their relative abundances within each plot and the mean values for each trait and each plot is computed. The relative abundance of species was calculated after excluding the cover and traits of each target species in the role of native or invasive dominant, to ensure that the resulting CWM trait values (for individual plots) are independent of both the cover and traits of target species and also of the total number of species—the analyses on CWM values display the proportions of traits within the community regardless of its species richness. The mean height of species, seed mass, specific leaf area (i.e., SLA), clonal reproduction, and life form (i.e., annual vs perennial) were used as the importance values for the CWM method. These traits represent a relatively complete, yet parsimonious, ecological and functional characterization of species (Westoby 1988, Divíšek et al. 2018). The information on height and life form was obtained from field guides (Armstrong 1915, Pojar and McKinnon 1994, Kershaw et al. 1998, Ladd and Oberle 2005). Data on seed mass were extracted from the Kew Seed Information Database. Data

on clonality and SLA were extracted from the TRY database (Kattge et al. 2011; see the list of original data papers in Appendix S6: Table S1), CLOPLA database (Klimešová et al. 2017) and from various online resources (Appendix S5: Table S1). Of the 598 species in our dataset, we acquired information on 471 species (79.0%) for SLA, 558 species (93.3%) for clonality, 591 species (98.8%) for height, and seed mass data were found for all species.

*Testing the relations of the representation of traits within a community to the dominance of the target dominant species.*—The relationships of species richness and individual species' traits with the invasive/native dominants' cover were tested using linear mixed-effect (i.e., LME) models. The data were clustered in spatial blocks, the identity of which was used as the random grouping variable. This approach turned out to be a more efficient way of modeling the spatial correlations, as revealed by the comparisons of the Akaike Information Criteria (e.g., Lukacs et al. 2007), compared to modeling the spatial dependence as a continuous variable, using the GPS coordinates, standardized by the two continents. In these models, the cover of the target dominant species was used as the predictor variable, while species richness and CWM values of individual traits within plots were used as the response variables.

*Testing the differences between the native and invasive dominants, native and invaded ranges, and between the two opposing directions of invasions.*—Linear mixed-effect analyses of covariance were used to test the differences in the relationships of the dominant species' cover and species richness or CWM values between the native and invaded ranges and between the continents—Europe vs North America. In these models, the dominant species' cover was used as the continuous predictor variable, the native vs invaded range (i.e., Europe vs North America) was included as the factor predictor variable, and species richness or individual CWM traits were used as the response variables. Following this scheme, the differences between the native and invaded ranges or between the continents would be revealed by the significant interaction between the effect of the target dominants species' cover and the two-level factor predictor variable (i.e., native/invaded range, native/alien target dominant, and from Europe/from North America). The spatial

dependence of individual plots was modeled as a grouping variable, with the factor levels representing the individual spatial clusters of plots. The assumption of normality was tested using the Shapiro-Wilk tests and square root transformations were applied when necessary. The models were then checked visually by plotting the residuals against the fitted variables. All univariate models were run in the R software using the NLME package (Crawley 2007, R Development Core Team 2013).

*Testing the effects of the target dominants on the overall trait composition of the community.*—Ordination analyses were used to test the relationships between the dominance of the target species and the distribution of species in a community and their CWM values. The identity of spatial blocks were included as a covariable into all ordination models, and individual vegetation plots were permuted within each spatial block (block defining covariable; see Lepš and Šmilauer 2014) in order to make sure that comparisons of plots with high vs low dominance of the target dominant species were realized within homogeneous units. The target dominant species' cover was used as the predictor, while the relative abundance of species (expressed as their percentage covers) or the CWM values of the species' traits were used as the response variables in the ordination models.

Similarly to the univariate LME models on species richness and individual traits, multi-dimensional analyses of covariance were used to test the differences between the continents and between the native and invaded ranges of the dominant species. In these multivariate models, the interaction between the target dominant

species' cover and (1) range or (2) continent (native, invaded; North America, Europe, respectively) were used as the predictor variables, and the CWM values of individual traits were the response variables. All ordination models were run in the CANOCO 5 software (ter Braak and Šmilauer 2012, Lepš and Šmilauer 2014).

## RESULTS

### *Dominant species' impacts on species richness, species composition, and the representation of traits*

In North America, both native and invasive dominants had a significant negative impact on species richness (native dominants:  $P = 0.026$ ,  $T = -2.261$ ,  $DF_{\text{resid}} = 104$ ; invasive dominants:  $P < 0.01$ ,  $T = -8.503$ ,  $DF_{\text{resid}} = 97$ ; Table 1, see also Appendix S3: Table S1 for the LME estimates) and affected the trait and species composition (native dominants:  $P = 0.004$ , pseudo- $F = 6.9$  and  $P = 0.012$ , pseudo- $F = 1.3$ , respectively; invasive dominants:  $P = 0.002$ , pseudo- $F = 8.0$  and  $P = 0.008$ , pseudo- $F = 1.2$ , respectively; Table 1, Fig. 1, 2). In central Europe, the cover of native dominants was significantly related only to species composition ( $P = 0.024$ , pseudo- $F = 1.3$ ; Table 1), while that of invasive dominants significantly reduced species richness ( $P = 0.034$ ,  $T = -2.149$ ,  $DF_{\text{resid}} = 106$ ) and affected the trait composition ( $P = 0.004$ , pseudo- $F = 5.2$ , Fig. 3), but their effect on species composition was only marginally significant ( $P = 0.098$ , pseudo- $F = 1.2$ ).

The relationships between the dominance and species richness, as well as species and trait

Fig 1

Table 1. The relationship between the cover of subgroups of the dominant species and species richness, species composition, trait composition, and individual traits, represented by the community-weighted mean (CWM) values ( $P$ -values from LME models in case of species richness and individual traits, and  $P$ -values from the permutation tests in case of species and trait composition).

Species subgroup	Species richness	Species composition	Trait composition	Height	Clonality	Annuals	Perennials
Invaded range (North America)	<b>&lt;0.01</b> ↓	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b> ↓†	0.026↓†	<b>&lt;0.01</b> ↓†	<b>&lt;0.01</b> ↓†
Invaded range (Europe)	<b>0.034</b> ↓	0.098	<b>&lt;0.01</b>	n.s.	0.066	n.s.	n.s.
Native range (North America)	<b>0.026</b> ↓	<b>0.012</b>	<b>&lt;0.01</b>	n.s.	0.08	0.077	0.028†
Native range (Europe)	n.s.	<b>0.024</b>	n.s.	0.08	n.s.	n.s.	n.s.

Notes: Significant effects are in bold and the arrows indicate a positive or negative association with dominant species cover.  
 † Significant quadratic term in the relationship. Data for seed mass and SLA are omitted, as no significant relations at the subgroup level were found for these traits.

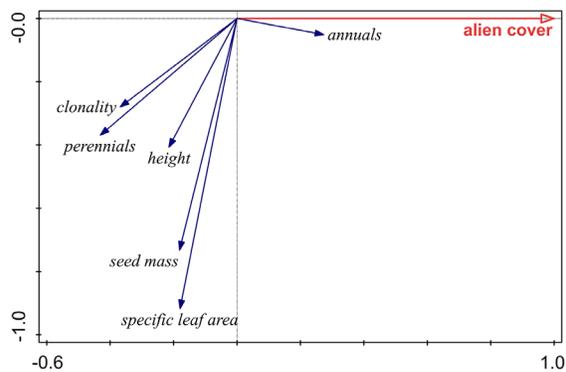


Fig. 1. Ordination plot (RDA, pseudo- $F = 8.0$ ,  $P = 0.002$ , first axis explains 6.4% of variability, the second axis explains 49.1%) on the distribution of individual species' traits (represented by the CWM values) in relation to the cover of the target invasive aliens of Eurasian origin in North America (i.e., *Agrostis capillaris*, *Bromus tectorum*, and *Cirsium arvense*). The plot shows a positive relation between the cover of Eurasian invaders and the share of annuals and a negative relation with the share of clonal and perennial species.

composition were not consistent across individual species. *Aster novi-belgii* and *Lupinus polyphyllus* showed a significant negative relationship between their cover and species richness in their native range, North America (*Aster novi-belgii*:  $P = 0.009$ ,  $T = -2.74$ ,  $DF_{\text{resid}} = 34$ ; *Lupinus polyphyllus*:  $P = 0.013$ ,  $T = -2.596$ ,  $DF_{\text{resid}} = 37$ ), but showed no significant effect on species and trait composition (Table 2, also see Appendix S4: Table S1 for the LME estimates). However, the cover of *Aster novi-belgii* had a significant positive quadratic relationship with SLA in North America ( $P = 0.043$ ,  $T = 2.102$ ,  $DF_{\text{resid}} = 34$ ). On the contrary, the cover of *Bromus tectorum* and *Solidago canadensis* was not related to species richness in Europe, but caused changes in species composition ( $P = 0.016$ , pseudo- $F = 1.5$  and  $P = 0.012$ , pseudo- $F = 1.4$ ; Table 2). Additionally, there was a positive quadratic relationship between the cover of *Solidago canadensis* and SLA in Europe ( $P = 0.046$ ,  $T = 2.073$ ,  $DF_{\text{resid}} = 33$ ).

Concerning individual traits, there was a negative quadratic relationship between the dominance of Eurasian invaders in North America and the height of species in invaded

communities ( $P = 0.004$ ,  $T = -2.927$ ,  $DF_{\text{resid}} = 96$ ), their ability of clonal spread ( $P = 0.026$ ,  $T = -2.263$ ,  $DF_{\text{resid}} = 96$ ), representation of perennials ( $P = <0.01$ ,  $T = -3.4322$ ,  $DF_{\text{resid}} = 96$ ), and a quadratic positive relationship with the representation of annuals ( $P = 0.004$ ,  $T = 2.955$ ,  $DF_{\text{resid}} = 96$ ). The constrained ordination analysis (RDA, pseudo- $F = 8.0$ ,  $P = 0.002$ ) confirmed the basic pattern of the relation between the cover of Eurasian dominants in North America and trait composition of the invaded community, showing a negative relation with the representation of clonal species, perennials, and tall species and a positive relation to the share of annuals. The cover of native dominants in North America resulted in a decrease in the representation of perennials ( $P = 0.028$ ,  $T = -2.2234$ ,  $DF_{\text{resid}} = 103$ ) and clonal species, with the latter relationship being only marginally significant ( $P = 0.08$ ,  $T = -1.76766$ ,  $DF_{\text{resid}} = 103$ ), and was positively associated with the representation of annuals ( $P = 0.077$ ,  $T = 1.788919$ ,  $DF_{\text{resid}} = 103$ ).

#### Differences between the dominant species' native and invaded ranges and between native and invasive dominants

The North American species invasive in Europe had similar impact on species richness in their native and invaded ranges ( $P = 0.3793$ ,  $T = 0.881$ ,  $DF_{\text{resid}} = 208$ , Table 3) but their impact on the trait composition differed ( $P = 0.002$ , pseudo- $F = 5.4$ , Table 3, Fig. 4).

In contrast, the results differed for the opposite direction of invasion (Fig. 5). The cover of Eurasian species invasive in North America affected species richness and trait composition of the recipient communities, especially the representation of life forms and clonal species, more in their invaded compared to their native range (species richness:  $P = <0.01$ ,  $T = -5.234$ ,  $DF_{\text{resid}} = 200$ ; trait composition:  $P = 0.004$ , pseudo- $F = 4.5$ ; representation of annuals:  $P = 0.016$ ,  $T = 2.421$ ,  $DF_{\text{resid}} = 198$ ; representation of clonals:  $P = 0.0545$ ,  $T = -1.934$ ,  $DF_{\text{resid}} = 198$ ; Table 3).

In the same vein, native and invasive dominants in North America differed in their impact on species richness and trait composition (species richness:  $P = <0.001$ ,  $T = -4.965$ ,  $DF_{\text{resid}} = 201$ ; trait composition:  $P = 0.002$ , pseudo- $F = 5.4$ , Table 3). However, only a marginally significant

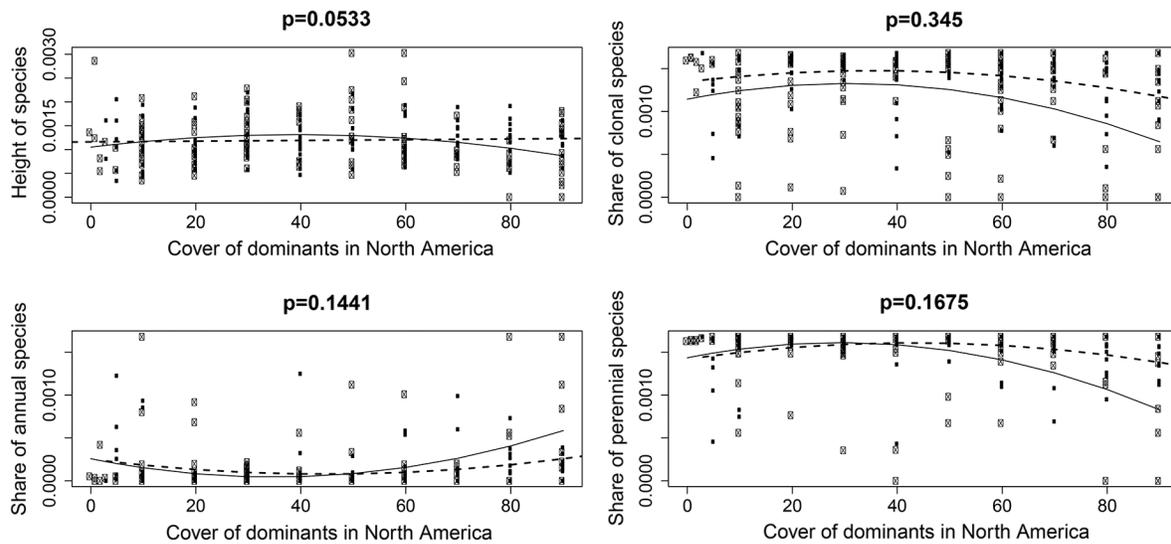


Fig. 2. The relation of the target dominants' cover with the height of species and with the share of clonal, annual, and perennial species. Data from North America are displayed, comparing the impacts of native (dashed line, solid symbols) and invasive dominants (solid line, crossed symbols). The heading above the plot depicts the significance of the difference between the two expressed relations.

difference in the effect on species' height was detected at the level of individual traits ( $P = 0.0533$ ,  $T = -1.944$ ,  $DF_{\text{resid}} = 199$ ). For native and invasive dominants in Europe, an

overall significant difference was found in the impact on trait composition ( $P = 0.01$ , pseudo- $F = 4.4$ ) but not at the level of individual traits (Table 3).

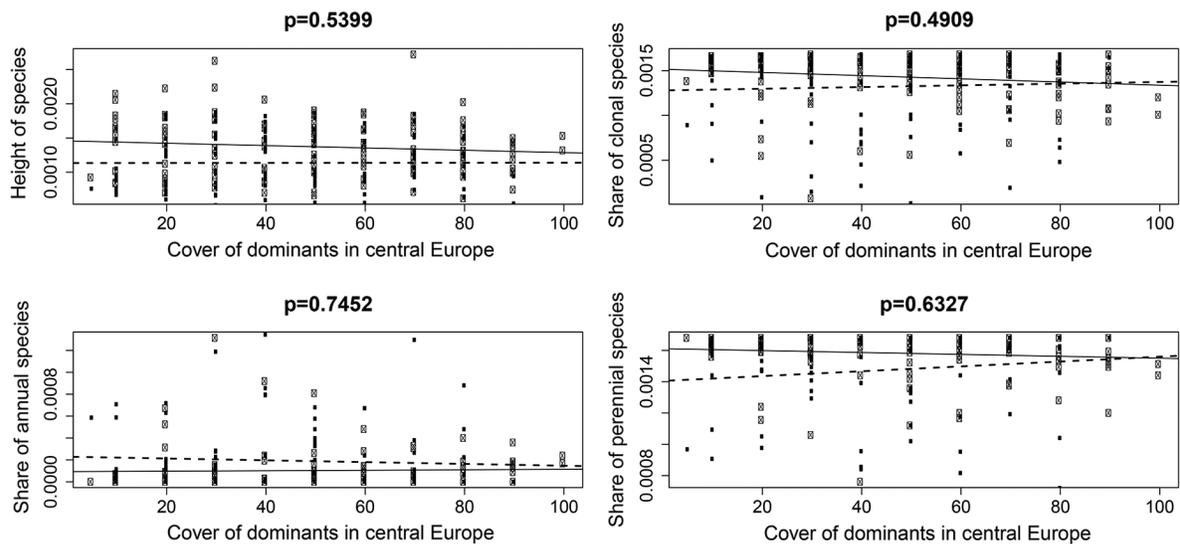


Fig. 3. The relation of the target dominants' cover with the height of species and with the share of clonal, annual, and perennial species. The data from central Europe are displayed, comparing the impacts of the native versus invasive dominants (dashed line with solid symbols, native dominants; solid line with crossed symbols, invasive dominants). The heading above the plot depicts the significance of the difference between the two expressed relations.

Table 2. The relationships between the cover of dominant species and species richness, species composition, and trait composition ( $P$ -values from LME models for species richness and individual traits, and  $P$ -values from the permutation tests for species and trait composition).

Dominant	Range	Species richness	Species composition	Trait composition	Height	Seed mass	SLA	Annuals	Perennials
<i>Agrostis capillaris</i>	<b>EU</b>	0.010↓	n.s.	n.s.	0.085	n.s.	n.s.	n.s.	n.s.
<i>Agrostis capillaris</i>	<b>NA</b>	<0.001↓	0.056	n.s.	<0.01↓†	<0.001↓†	0.034↓†	n.s.	n.s.
<i>Bromus tectorum</i>	<b>EU</b>	n.s.	0.016	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Bromus tectorum</i>	<b>NA</b>	<0.001↓	n.s.	0.034	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Cirsium arvense</i>	<b>EU</b>	n.s.	n.s.	n.s.	0.053	n.s.	n.s.	n.s.	n.s.
<i>Cirsium arvense</i>	<b>NA</b>	<0.001↓	<0.01	n.s.	0.078	n.s.	0.038↓†	<0.01↓†	<0.01↓†
<i>Aster novi-belgii</i>	<b>EU</b>	0.013↓	n.s.	0.014	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Aster novi-belgii</i>	<b>NA</b>	<0.01↓†	n.s.	n.s.	n.s.	n.s.	0.043↓†	n.s.	n.s.
<i>Lupinus polyphyllus</i>	<b>EU</b>	<0.001↓	n.s.	<0.01	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Lupinus polyphyllus</i>	<b>NA</b>	0.013↓†	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Solidago canadensis</i>	<b>EU</b>	n.s.	0.012	n.s.	n.s.	n.s.	0.046↓†	n.s.	n.s.
<i>Solidago canadensis</i>	<b>NA</b>	0.039↓	n.s.	<0.01	n.s.	n.s.	<0.01↓†	0.029↓†	0.015↓†

Notes: The representation of individual traits is expressed by the community-weighted means (CWM). EU, Europe; NA, North America. The arrows indicate a positive or negative association with dominant species cover. Native range is in boldface.

† Significant quadratic term in the relationship. Data for clonality were omitted as no significant relations were found between the cover of individual dominants and the representation of clonal species.

#### Differences associated with the direction of invasion

Eurasian dominants in North America exhibited stronger impacts on species richness than North American dominants in Europe ( $P = <0.001$ ,  $T = -4.4575$ ,  $DF_{\text{resid}} = 203$ ). There were also differences associated with the direction of invasion in the impacts on trait composition ( $P = 0.002$ , pseudo- $F = 4.9$ ; Table 3). Invaders in North America had a stronger positive impact on the representation of annuals and stronger negative impact on perennials and clonal species than North American invaders in

Europe (Fig. 6), with the difference in the latter being only marginally significant (annuals:  $P = 0.007$ ,  $T = 2.704$ ,  $DF_{\text{resid}} = 201$ ; perennials:  $P = 0.003$ ,  $T = -2.975$ ,  $DF_{\text{resid}} = 201$ ; clonals:  $P = 0.093$ ,  $T = -1.686$ ,  $DF_{\text{resid}} = 201$ ; Table 3).

## DISCUSSION

#### Dominant species' impacts on species richness, species composition, and the representation of traits

In general, different aspects of the impacts of dominant species are consistent: impacts on

Table 3. Differences in the relationships between the cover of the target dominant species' subgroups and species richness, species and trait composition, as well as the individual traits, represented by the community-weighted mean (CWM) values ( $P$ -values from the LME ANCOVAs in case of species richness and individual traits, and  $P$ -values from the permutation tests from multi-dimensional ordination ANCOVAs in case of trait composition).

Compared subgroups	Richness	Traits	Height	Clonality	Annuals	Perennials
Native × invaded range (from NA to EU)	n.s.	<0.01	n.s.	n.s.	0.094	0.055
Native × invaded range (from EU to NA)	<0.001	<0.01	n.s.	0.055	0.016	<0.01
Aliens in NA × aliens in EU	<0.001	<0.01	n.s.	0.093	<0.01	<0.01
Native × invasive dominants (EU)	n.s.	0.1	n.s.	n.s.	n.s.	n.s.
Native × invasive dominants (NA)	n.s.	<0.01	0.053	n.s.	n.s.	n.s.

Notes: NA, North America; EU, Europe. A significant difference indicates a stronger relation in the invaded range compared to the native range (row 2), for the Eurasian aliens in North America compared to North American aliens in Europe (row 3), and for the invasive dominants compared to native dominants in North America (row 5). Data for seed mass and SLA were omitted from the table, as no significant differences in the representation of these traits were found.

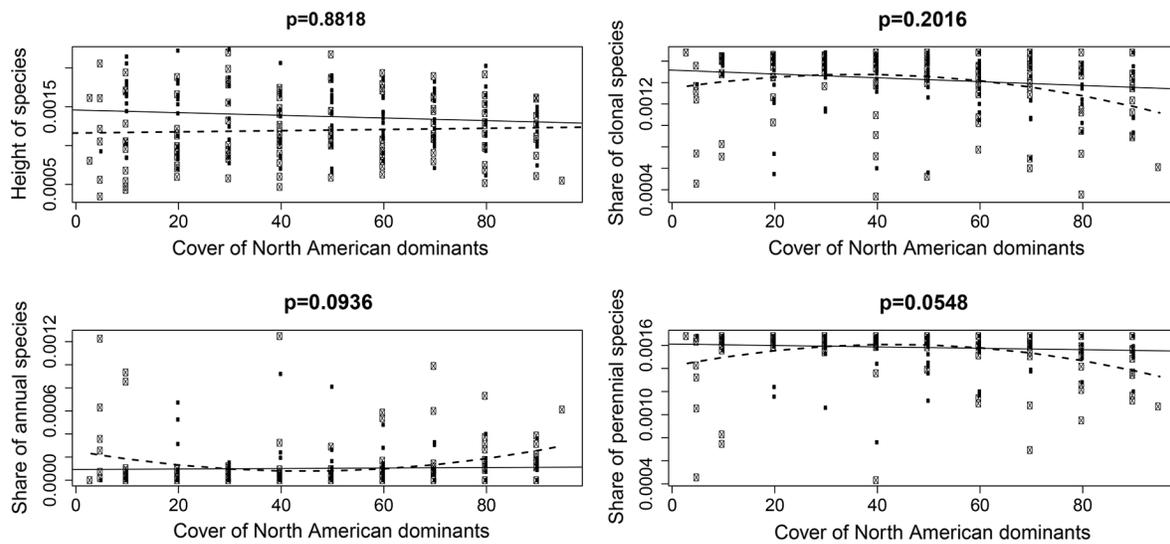


Fig. 4. Data for North American dominants, comparing the relations of their cover with the height of the community and with the share of clonal, annual, and perennial species in the native (dashed line, solid symbols) and invaded ranges (solid line, crossed symbols). The heading above the plot depicts the significance of the difference between the two expressed relations.

species richness act in concert with those on trait composition, reflecting that species functional traits relate to their ability to coexist with both native and invasive dominants. However,

exceptions to this rule have been found for individual dominants. In North America, the native *Lupinus polyphyllus* reduces species richness without any obvious effects on the composition

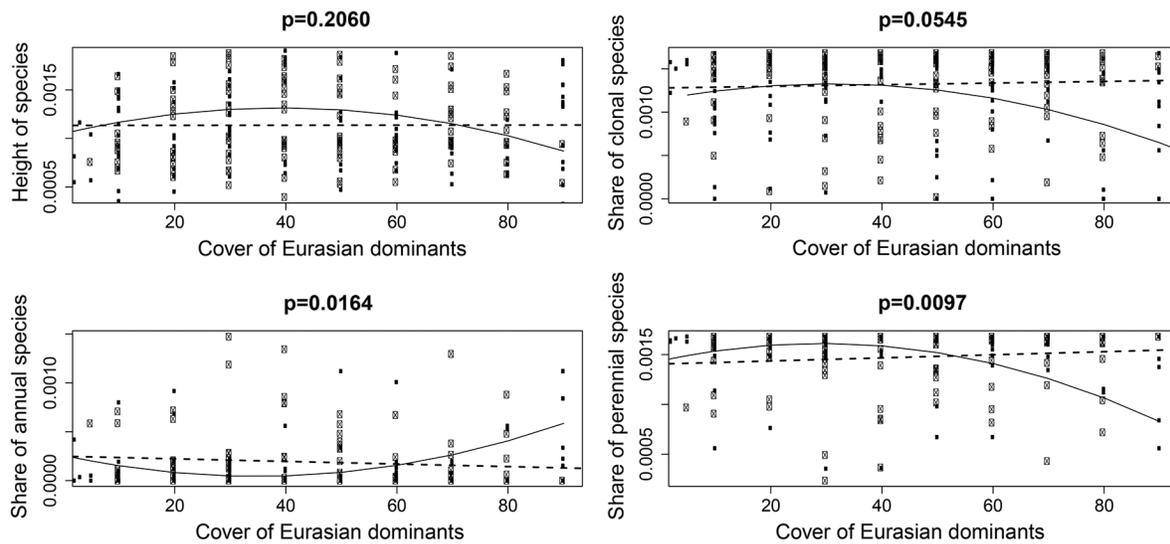


Fig. 5. Data for Eurasian dominants, comparing the relations of their cover with the height of the community and with the share of clonal, annual, and perennial species in the native (dashed line, solid symbols) and invaded ranges (solid line, crossed symbols). The heading above the plot depicts the significance of the difference between the two expressed relations.

of species traits, suggesting that its dominance has little or no effect on the representation of the selected traits within the community.

As such, it is clear that the traits of native species play a key role in the reduction of species richness resulting from invasions, and species loss is thus not a random process (Chabrierie et al. 2010, Hejda 2013b, Bravo-Monasterio et al. 2016, Florianová and Münzbergová 2016, Smith et al. 2016, Flinn et al. 2017, Hejda et al. 2017). In addition to the overall negative impact on native species richness (Hejda et al. 2009, Pyšek et al. 2012), invasive species can also suppress some native species more than others, and native species with certain characteristics can even benefit from invasions. For example, the invasion of *Pinus contorta* in Patagonia, southern Chile, favors shade-tolerant species with a conservative reproduction strategy (Bravo-Monasterio et al. 2016). Similarly, the invasive *Prunus serotina* promotes shade-tolerant, short-living ruderals and early spring geophytes, but suppresses light-demanding graminoids and native woody species (Chabrierie et al. 2010). Further, it has been proposed that it is the trait distance between the invader and native species that determines the outcome of an invasion, rather than the absolute

values of the invader's traits (Hejda et al. 2009, Fried et al. 2014, Lee et al. 2016). However, it is still debated whether it is more advantageous for natives to be ecologically similar to the invader and compete with it successfully, or to adopt a contrasting strategy to avoid direct competition. Recently, Divíšek et al. (2018) showed that this depends on the invasion stage—naturalized species in central European habitats tend to be similar in their functional traits to native members of the community, while to become invasive, the species need to possess different traits. This idea is supported by the results of a case study on the invasive herb *Impatiens glandulifera*, which brought new characteristics into the invaded community, such as tall stature, high SLA, and a low leaf dry matter content (LDMC; Helsen et al. 2018). On the other hand, Funk et al. (2016) demonstrated that invaders in the Mediterranean region tend to be similar to native species in terms of their life-form.

Our results suggest that species ecologically similar to the dominants of communities in which they grow (clonal perennials in our case) are most suppressed, while those with contrasting ecological characteristics (annuals) escape the suppressive effect of the dominant species.

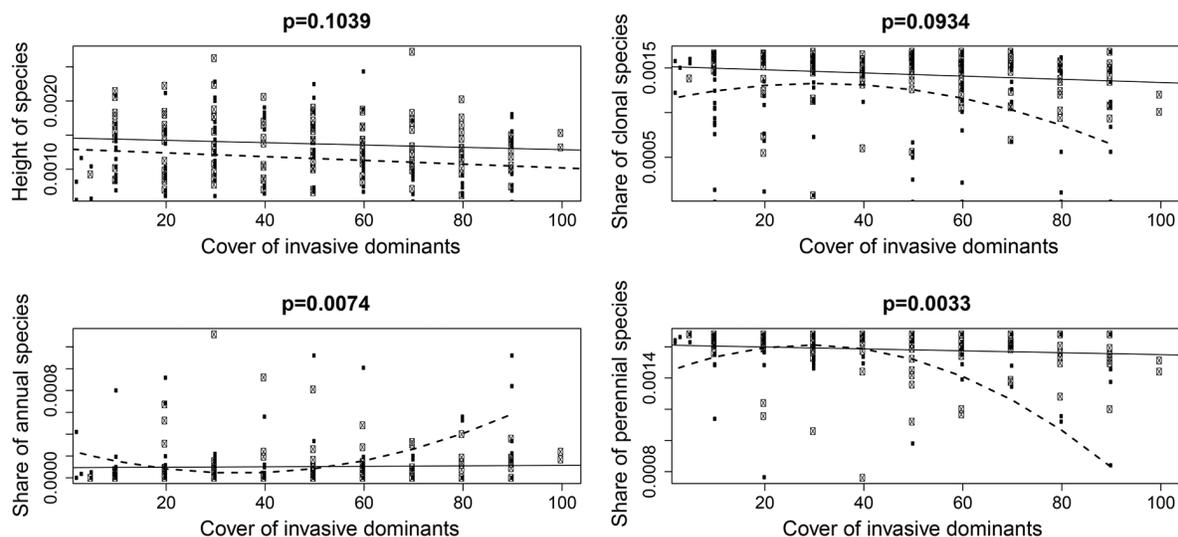


Fig. 6. Data for Eurasian dominants and North American dominants (dashed line with solid symbols and solid line with crossed symbols, respectively), comparing the relations of their cover with the height of the community and with the share of clonal, annual, and perennial species in their invaded ranges (North America and Europe, respectively). The heading above the plot depicts the significance of the difference between the two expressed relations.

Further, this rule seems to hold regardless of whether the dominant is native or alien in a given area.

#### *Differences between the dominant species' native and invaded ranges and between native and invasive dominants*

In our study, the Eurasian invaders in North America suppressed perennials and clonal species and, on the contrary, their invasion resulted in an increase of the share of annuals. In the same vein, ordination analyses showed a significant impact of Eurasian invasive dominants on the trait composition in North America and a negative relation between the invaders' cover and the representation of tall, clonal, and perennial species. One of the three studied invaders in North America (*Bromus tectorum*) is a non-clonal annual and was not found to affect the representation of clonal or perennial species in the invaded communities. Therefore, it is likely that the effects of the Eurasian invaders in North America, detected by our models, were mainly caused by *Cirsium arvense*, as the other clonal perennial Eurasian invader within our selection, *Agrostis capillaris*, was not found to affect the representation of either clonal or perennial species in North America. Similar to native dominants, the suppressive effect of the Eurasian invader on the clonal and perennial species in North America is likely caused by the interspecific competition with the dominant species of the same life history (see also Hejda et al. 2009).

In terms of individual traits, invasive species in North America suppress the height of resident communities, by eliminating tall species, and they tend to eliminate clonal perennials and encourage the occurrence of annuals. Interestingly, native dominants in North America had similar effects, with their increasing cover resulting in the decrease of perennials and clonal species, and increase of annuals, although these effects were weaker.

The effects of native and invasive dominant species in Europe are less straightforward. Although native European dominants have some effect on the composition of a community, they do not seem to reduce the species richness or affect the composition of traits. Dominant species only rarely outcompete co-occurring species in Europe, perhaps due to their long-term

adaptation to pastoral management and intensive competition. This is in contrary to the species of North American origin (Larson et al. 2001, MacDougall et al. 2018).

The Eurasian invasive dominants in North America (as well as native dominants to a degree) relate quadratically rather than linearly to the representation of traits such as height, clonality, and life form (Fig. 2). Interestingly, *Lupinus polyphyllus* and *Aster novi-belgii* (both native to North America) also relate quadratically negatively to species richness in their native range (see Hejda et al. 2017 for details). It is apparent that neither species richness nor traits such as height, clonality, or perennial life form show any suppression or exhibit even a positive relation to the dominants' cover, until some threshold value of its dominance is reached, and then the relationships change to negative (see also Sofaer et al. 2018).

#### *Differences associated with the direction of invasion*

We show that differences in the impacts of native and invasive dominants, as well as differences between the dominant species' native and invaded ranges, vary according to the direction of invasion. In central Europe, native and invasive dominants differ in their impacts on the composition of traits, but not on species richness. In North America, invasive dominants reduced species richness and affected the trait composition more than native dominants. Additionally, the Eurasian dominants reduced species richness and affected the trait composition more in their invaded than in the native range. Multi-dimensional analyses of covariance confirmed stronger impacts of Eurasian invaders on the trait composition of vegetation in North America, compared to their impacts in the native range, to the impacts of native North American dominants, and to the impacts of North American invaders in Europe. On the contrary, dominants of North American origin did not differ in their impacts on species richness in both ranges. Further, the multi-dimensional analyses of covariance showed that North American species had stronger impacts on trait composition in their native range.

The fact that Eurasian invaders in North America have stronger impacts than North

American invaders in Europe is in accordance with the Neolithic plant invasion hypothesis (NPIH; MacDougall et al. 2018, see also di Castri 1989). European plants have been exposed to intensive human activity since the Neolithic era (c. 7000 BC in Europe). This may have played a crucial role in the ability of Eurasian species to outcompete native species worldwide (di Castri 1989, Callaway et al. 2008, La Sorte and Pyšek 2009, MacDougall et al. 2018). Therefore, the success of European invasive species in North America may be at least partly attributed to the evolutionary naivety of North American species. Further, the orientation of mountain ranges in Europe may have facilitated the long-distance east–west migrations during the glacial periods, making it possible for the Eurasian species to interact with a broader spectra of species and environments, which may have also contributed to the competitive vigor of Eurasian species (di Castri 1989, Sax and Brown 2000, Seastedt and Pyšek 2011, Fridley 2013). Moreover, most prairies in North America are nowadays overgrazed and the European plant species are better adapted to intensive grazing (Mack 1981, Seastedt and Pyšek 2011).

However, our North American study sites contained a limited selection of species of European origin (besides the target dominants), and therefore the studied dominants of European origin interacted with some species that occurred in both ranges. On the contrary, this situation was very rare in European study sites, where the sampled communities usually did not contain any species of North American origin, besides the target dominant. However, this further supports that it is actually the difference in competitive vigor of Eurasian versus North American species that made the aliens impacts in the North America stronger compared to those in Europe.

Therefore, the direction of invasion is an important feature that needs to be taken into account. These conclusions would be more robust if both groups of invasive species, defined according to their direction of invasion, included only clonal perennials or a balanced combination of annuals and clonal perennials. However, when we were selecting the target dominant species for this study, the criteria of reaching a similar magnitude of dominance in comparable habitats on both continents was considered as

superior to that of having equal representation of life forms.

## CONCLUSIONS

Our results indicate that the biogeographic aspect, represented by the reciprocal direction of invasion in our study, is an important factor of the overall impacts of invasive species. In particular, the inter-continental setup representing the exchange between the Old World and New World points to a difference in the impacts of invasions, similar to that between continents and islands (see, e.g., Jaeger et al. 2007 and Pyšek et al. 2012, 2017). The results also show the importance of trait-based approaches which can bring more detailed insights into the mechanisms of invasive species impact, including the long-persisting question of whether it is more advantageous for native species to be similar to the invader and compete with it or to possess different ecological traits to avoid direct competition (Hejda and de Bello 2013).

## ACKNOWLEDGMENTS

The study was supported by EXPRO (grant no. 19-28807X, Czech Science Foundation) and long-term research development project RVO 67985939 (The Czech Academy of Sciences). TRY initiative on plant traits (<http://www.try-db.org>) kindly provided us with some data on species traits. The TRY initiative and database is hosted, maintained, and developed by J. Kattge and G. Bönisch (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY is currently supported by DIVERSITAS/Future Earth and German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig. We thank Desika Moodley for improving our English and providing important feedback.

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