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Dominance has a biogeographical component: do plants tend to exert stronger impacts in their invaded rather than native range?

Martin Hejda^{1*}, Kateřina Štajerová^{1,2} and Petr Pyšek^{1,2}

¹Department of Invasion Ecology, Institute of Botany, The Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic,
²Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Prague, Czech Republic

ABSTRACT

Aim Using three North American species invading Europe (*Aster novi-belgii*, *Lupinus polyphyllus* and *Solidago canadensis*) and three European species invading North America (*Agrostis capillaris*, *Bromus tectorum* and *Cirsium arvense*), we tested (1) whether the dominant species impact differs between its native and invaded ranges and (2) whether the impacts differ according to the direction of invasion (from Europe to North America and vice versa).

Location North America (USA) and central Europe (Czech Republic).

Methods The dominance of the selected species was expressed as its relative cover, and its relationship to species richness was tested using marginal and mixed-effect regression models.

Results All the three North American species invading Europe suppressed species richness in the native range, while only two (*A. novi-belgii* and *L. polyphyllus*) impacted native species richness in the invaded range. On the contrary, of the three European species invading North America, only *A. capillaris* was found to suppress species richness in its native range, while all three suppressed it in the invaded range. Overall, the richness of native species responded significantly more negatively to the dominant species cover in its invaded rather than native range, regardless of the identity of the dominant species.

Main conclusions Invasive species suppress diversity more in the invaded range, and European invaders have more profound impacts in North America than North American invaders in Europe. We suggest that long-term coexistence and species filtering are responsible for the lower impacts in the native range, while large-scale evolutionary patterns are likely to be associated with the more profound impacts of selected European species as invaders in North America than vice versa.

Keywords

diversity, dominant species, impact, invaded range, invasive species, native range

*Correspondence: Martin Hejda, Department of Invasion Ecology, Institute of Botany, The Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic.
E-mail: martin.hejda@ibot.cas.cz

INTRODUCTION

Invasions by alien plants are regarded as one of the most important anthropogenic changes affecting diversity, composition and functioning of communities and ecosystems worldwide (Mack *et al.*, 2000; Pyšek *et al.*, 2012; Gaertner *et al.*, 2014; van Kleunen *et al.*, 2015). At the community scale, the dominance of invasive species tends to eliminate native species or transform the site conditions in a way that causes replacement of native species by widespread ruderal

or synanthropic species (see e.g. Hulme & Bremner, 2006; Hejda & Pyšek, 2006; Jäger *et al.*, 2007; Hejda *et al.*, 2009). At the macroecological scale, the spread of invasive aliens tends to homogenize local and regional floras (McKinney & Lockwood, 1999; Winter *et al.*, 2009).

However, some species become distinctive dominants even in their native ranges (Walker *et al.*, 1999; Ervin & Wetzel, 2002). Especially communities occurring at sites with high resource levels and low stress tend to be dominated by one or a few species that are capable of producing high amount

of biomass (Walker *et al.*, 1999). The relationship between productivity and diversity, one of the most important postulates in modern community ecology (Tilman, 1999; Cox, 2004; Lanta & Lepš, 2006; Guo, 2007; Pekin *et al.*, 2012), presumes that highly productive sites tend to be dominated by a single or a few species, which suppress community diversity, regardless of whether the dominant species is native or alien. However, species can be assumed to perform better in the presence of a native dominant species due to a long history of coexistence (Cox, 2004; Shah *et al.*, 2014). Communities in the dominant species native range may be more diverse, as species are adapted to coexist with that particular dominant species. On the contrary, alien dominant species represent a novel element to invaded communities. Therefore, communities with alien dominants are likely to be more impacted, especially if the invading species is a strong dominant compared to the most abundant native species in that particular community (Hejda *et al.*, 2009).

However, patterns between native and invaded ranges can be further complicated by large-scale evolutionary effects, such as that species from one region can be stronger competitors than those from another region (di Castri, 1989; Pyšek *et al.*, 2009; Stohlgren *et al.*, 2011). This is observed, for example, on islands, where native species are especially prone to being eliminated from the invaded communities (Pyšek *et al.*, 2012), but the same mechanism seems to hold for the whole continents as well; for example, many native Australian species can be considered evolutionarily naïve compared with invaders from southern Europe, Africa or South America (Mooney & Drake, 1989; Williams & West, 2000). Some evidence suggests a similar pattern between Europe and North America – even though the basic climate of these areas is similar, North American species appear to be sensitive to competition from European invaders (Seastedt & Pyšek, 2011).

One of the reasons is probably the long-term adaptation of Eurasian species to human-induced changes of landscape

and biological communities (di Castri, 1989; Sax & Brown, 2000; Stohlgren *et al.*, 2011), as invasions by European species were supported by European colonization worldwide and accompanied by the adoption of European landscape management (di Castri, 1989; Seastedt & Pyšek, 2011).

In this study, we use three European species that are invasive in North America, and three North American species that are invasive in Europe, each of them being a strong dominant in both its native and invaded ranges, to explore (1) whether their impacts on species richness of plant communities differ in the native versus invaded range. In addition, (2) we test what is the effect of the geographical direction of invasion, by comparing whether the impact on species richness of European invaders in North America differs from that of North American invaders in Europe.

MATERIALS AND METHODS

Sampling

Three species native to Europe and invasive in North America [*Agrostis capillaris* L., *Bromus tectorum* L. and *Cirsium arvense* (L.) Scop.] and three species invading from North America to central Europe (*Aster novi-belgii* L., *Lupinus polyphyllus* Lindl. and *Solidago canadensis* L.) were selected for this study. The aim was to focus on species capable of reaching a high degree of dominance in both ranges (Table 1). This condition proved to be more restrictive for European species, as many European invaders that form large continuous stands in North America are not distinctive dominants in Europe. Further, the focus was on species that are not restricted to strongly disturbed habitats in either the native or invaded ranges. Finally, we paid attention to select species that reach a high dominance in similar habitats in the two ranges, as our previous study showed that habitats occupied in the native range can differ from those occupied in the

Table 1 Basic characteristics of the species studied and their native- and invaded-range habitats in North America and central Europe, where the vegetation was sampled.

Dominant species	Family	Origin	Life-form	Native-range habitats	Invaded-range habitats
<i>Aster novi-belgii</i>	Asteraceae	NE North America	RPP	Moist, eutrophic tall-forb vegetation on ruderalized meadows and ditches, riparian tall-forb stands	Ruderalized meadows, riparian tall-forb stands, eutrophic and wet vegetation
<i>Lupinus polyphyllus</i>	Fabaceae	NW North America	RPP	Ruderalized meadows, riparian tall-forb stands	Mesic to moist submontane and montane meadows with a degree of ruderalization, mostly on acidic soil
<i>Solidago canadensis</i>	Asteraceae	NE North America	RPP	Mesic to moist meadows, with a degree of ruderalization	Ruderalized or abandoned meadows, roadsides
<i>Agrostis capillaris</i>	Poaceae	Europe	PP	Submontane meadows on acidic soil	Moist to dry grasslands and roadsides, grasslands on sandy, acidic soil
<i>Bromus tectorum</i>	Poaceae	Europe, SE to central Asia	AN	Dry sandy and continental grasslands, sometimes near railroads	Dry grasslands and rangelands, dry roadside grasslands
<i>Cirsium arvense</i>	Asteraceae	Eurasia	PP	Ruderalized or abandoned meadows and meadow edges	Tallgrass prairies with a short history of disturbance

AN = annual, RPP = rhizomatous polycarpic perennial, PP = polycarpic perennial.

invaded range (Hejda *et al.*, 2009, 2015). The descriptions of habitats where the vegetation was sampled are presented in Table 1. Given the limited number of species meeting these conditions, we did not aim at evaluating the effect of life-forms on the processes studied because we were not able to identify enough representatives for each of them.

The dominance was expressed as the species percentage cover, which is considered to be related to its biomass (Arvid, 2000; Roetgermann *et al.*, 2000; Muukkonen *et al.*, 2006). Data sampling biases were eliminated by a single researcher sampling in both ranges.

In both ranges (Colorado, Idaho, Maine, North Dakota, Oregon, Utah, Washington State and Wyoming representing North America; and the Czech Republic, representing central Europe), vegetation plots of 2 × 2 m in size and with varying cover of the dominant species (native or invasive) were sampled. This plot size allowed us to test the ability of other species in the plant community to occur within the closed stands of the dominant species, rather than between its patches. Each of the six species under study was sampled in 40 plots in North America and 40 plots in central Europe, making 480 vegetation plots altogether – 6 focal species × 2 ranges × 40 plots per each species within either native or invaded range. Plots were clustered in spatially defined groups, each group representing a single population of the target dominant species. The sampled populations (spatial clusters) differed substantially in size, leading to different numbers of plots per population (cluster) and therefore also different numbers of populations (clusters) per species/range. The brief descriptions of habitats where the vegetation was sampled are presented in Table S5 in Appendix S1. Only large populations, occurring with a gradient of the dominant species cover, could have been included in our sampling scheme. Within each population (cluster), plots were spaced non-randomly to obtain a balanced set of plots with low,

intermediate and high cover of the dominant species. Occasionally, other alien species were also present in plots, besides the target dominant species, especially in the invaded range. However, the plots were chosen so that the other aliens reached only very small covers and were therefore unlikely to affect the species diversity of the sampled community. The numbers of sampled populations for each species within a given range are listed in Table 2. The relative abundance of all species was expressed as estimates of their percentage cover, even though the species richness, expressed as simple number of native species present, was of the most interest. In many cases, it was not possible to determine plants to the species level; however, it was still possible to judge their native/alien status. Such plants were included in the calculation of species richness, if considered native. On the contrary, both native and alien species of the shrub or tree layer, which were present on few plots, were excluded from the analyses. Woody species in general are less likely to be impacted by the dominance of herbaceous species, or their impact is apparent after many years, given the long-term generation times of woody species. The species were determined and their origin judged using fieldguides (Armstrong, 1915; Pojar & MacKinnon, 1994; Niering *et al.*, 2001).

Data analysis

The relationships between the target species dominance (expressed as percentage cover) and the richness of native species in the given region (North America or central Europe) were tested using marginal regression models. The spatial distribution of plots was included as a residual correlation structure. The models with factors representing spatial clusters were compared with those where the spatial autocorrelation was included as a continuous variable (using standardized GPS coordinates and Gaussian spatial

Table 2 Marginal regression models of the relationships between the cover of dominant species invading from North America to Europe (*Aster novi-belgii*, *Lupinus polyphyllus*, *Solidago canadensis*) and invading from Europe to North America (*Agrostis capillaris*, *Bromus tectorum*, *Cirsium arvense*), and richness of native species. The column 'Overall correlation' shows correlation coefficients counted for the whole subset of the data, regardless on the spatially defined autocorrelation structure. The column 'No. of populations' shows the number of spatial clusters, which are considered a residual autocorrelation factor within the marginal regression models. Raw numbers of species were used as a response variable in these models.

Dominant species	Origin	Range	Overall correlation	No. of populations	Estimate (marginal models)	P-value
<i>Aster novi-belgii</i>	North America	Native (USA)	−0.4066	4	−0.0018x ² + 0.1198x + 8.1713	0.0094
<i>Aster novi-belgii</i>	North America	Invaded (CZ)	−0.437	5	−0.0070x + 3.2474	0.013
<i>Lupinus polyphyllus</i>	North America	Native (USA)	0.1392	7	−0.0010x ² + 0.103x + 6.1055	0.013
<i>Lupinus polyphyllus</i>	North America	Invaded (CZ)	−0.2635	4	−0.0016x + 1.2679	< 0.001
<i>Solidago canadensis</i>	North America	Native (USA)	−0.1043	4	−0.0435x + 12.7860	0.039
<i>Solidago canadensis</i>	North America	Invaded (CZ)	−0.0136	5	0.0003x + 2.7395	n.s.
<i>Agrostis capillaris</i>	Europe	Invaded (USA)	−0.5842	10	−0.073103x + 10.1274	< 0.001
<i>Agrostis capillaris</i>	Europe	Native (CZ)	−0.3550	5	−0.0023x + 1.1576	0.010
<i>Bromus tectorum</i>	Europe	Invaded (USA)	−0.5719	10	−0.0145x + 1.5273	< 0.001
<i>Bromus tectorum</i>	Europe	Native (CZ)	−0.0557	6	0.0042x + 12.1468	n.s.
<i>Cirsium arvense</i>	Eurasia	Invaded (USA)	−0.6580	3	−0.0151x + 2.5050	< 0.001
<i>Cirsium arvense</i>	Eurasia	Native (CZ)	0.1746	5	0.0010x + 0.8603	n.s.

autocorrelation function), but models with the factor variable turned out to be more parsimonious. The degree of parsimony, expressing the models' explanatory power compared with their complexity, was evaluated based on the Akaike information criterion (AIC – see e.g. Lukacs *et al.*, 2007). The assumptions about the distribution of data were based on the normal quantile probability plots and Shapiro–Wilk tests of normality (Crawley, 2007). When necessary, square root or logarithmic transformations were used to achieve the normality of data. If the normality of data could not be achieved using these transformations, non-normal marginal models (generalized estimating equations using the R function 'geeglm') were adopted.

The differences in the relationships between the cover of each target dominant species and native species richness between the two ranges (native versus invaded) were investigated using marginal models of analysis of covariance. The interaction between the dominant species cover and a two-level factor 'range' was of the most interest, as it tested whether the richness of native species responded differently to the cover of the dominant species in its native versus invaded range. The same as with the marginal regression models, spatial distribution of the plots was fitted as a factor variable and the degree of parsimony of various models (with or without quadratic terms, accounting or not accounting for heteroscedasticity between clusters) was evaluated based on the AIC. Contrary to the marginal regression models, marginal analyses of covariance compared vegetation between the ranges, often with different numbers of species in the plots, but the goal was to express differences in the proportions of species richness missing from the heavily dominated vegetation, rather than those in the simple numbers of species. For these reasons, we used the ratios between the numbers of species recorded in a particular plot and the intercept obtained from the marginal regression model for that particular species and range. The intercepts from marginal regression models served as estimates of species richness of the uninvaded community or the community without that particular dominant species. In short, raw numbers of species were used for the marginal regression models, counted separately for each species and range (Table 2), and the ratios between the numbers of species and intercepts from the marginal regressions were used for the analyses of covariance, comparing the effects between ranges (Tables 3 & 4).

Finally, a model including the whole dataset was created to test for the relationships between the dominant's cover and richness of native species, regardless on the identity of the dominant species. A lme ANCOVA was chosen, with a hierarchical arrangement of random factors (spatial clusters within each target dominant species, with the identity of the target dominant species being considered a random factor). The factors 'continent' (North America, central Europe), 'range' (native, invaded) and the dominant species cover were included as fixed variables. The interaction term between the effects of dominant species cover and 'range'

Table 3 Marginal analyses of covariance, evaluating differences in the relationships between species richness and the cover of species native to North America invading Europe (*Aster novi-belgii*, *Lupinus polyphyllus*, *Solidago canadensis*) and native to Europe invading North America (*Agrostis capillaris*, *Bromus tectorum*, *Cirsium arvense*). In these models, the ratios between the numbers of species and intercepts from the individual marginal regression models (Table 2) were used as response variables.

Dominant species	Estimate (North America)	Estimate (central Europe)	P-value (North America versus central Europe)
<i>Aster novi-belgii</i>	1.3959 – 0.0064x	1.0136 – 0.0039x	n.s.
<i>Lupinus polyphyllus</i>	1.2342 + 0.0018x	0.9948 – 0.0027x	0.053
<i>Solidago canadensis</i>	0.9049 – 0.0015x	1.0781 – 0.0004x	n.s.
<i>Agrostis capillaris</i>	1.0125 – 0.0074x	1.0109 – 0.0034x	0.004
<i>Bromus tectorum</i>	2.5263 – 0.0213x	1.0713 – 0.0019x	< 0.001
<i>Cirsium arvense</i>	1.0172 – 0.0099x	1.0413 + 0.0026x	0.001

expressed possible differences between the dominant species impacts in its native versus invaded range. The three-way interaction between the cover of dominant species, 'range' and 'continent' tested if the effects of dominant species in native versus invaded range differed between the two directions of invasion (from Europe to North America, from North America to Europe). Ratios between the numbers of species and intercepts from the marginal regression models

Table 4 Results of a LME model testing (1) the differences in the relationships between the dominant species cover and species richness in the native versus invaded range (represented by the interaction between the terms 'dominant species cover' and 'range') and (2) the effect of the direction of invasion – from North America to Europe (*Aster novi-belgii*, *Lupinus polyphyllus*, *Solidago canadensis*) and from Europe to North America (*Agrostis capillaris*, *Bromus tectorum*, *Cirsium arvense*) – on the impact of the alien dominant species on species richness. This is represented by the three-way interaction between the terms 'dominant species cover', 'continent' and 'range'. The ratios between the number of species recorded on a particular plot and the intercept from a corresponding marginal regression model (Table 2) were used as a response variable in this model.

Term (main effect or interaction)	P-value
Intercept	< 0.001
Dominant species cover	< 0.001
Continent (North America, central Europe)	0.006
Range (native, invaded)	0.063
Dominant species cover*continent	< 0.001
Cover*range	< 0.001
Continent*range	n.s.
Cover*continent*range	0.003

were used as a response variable. All analyses were performed using R (R Development Core Team, 2011), where the script for the overall lme model was: `lme(numbers of species/intercept from the regression model~dominant species' cover*continent*range, random = ~1|dominant species' identity/spatial cluster)`. The accuracy of all models was examined using the standardized residuals plotted against fitted values.

To account for at least some of the large-scale factors, possibly confounded with our transcontinental arrangement, we tested if the basic climatic characteristics differed between the two continents and between the native and invaded ranges of the dominant species. The effects of continent (North America, central Europe) and range (native, invaded) were tested separately, as these created different subsets of the data. The basic climatic characteristics (mean temperature, precipitation in the dry period, precipitation in the wet period) were expressed as PCO scores (Dupin *et al.*, 2011). Unfortunately, the climatic data could not be obtained at the within-population (cluster) level. Therefore, it was not possible to include the climatic data into either the marginal models or the LME – the climatic data would be confounded with the grouping variable. Therefore, separate linear models were created, with range or continent as predictors and climatic data as responses, to test (1) whether the basic climatic characteristics differed between the two ranges and continents and (2) whether the climatic characteristics related to species richness. Each population (cluster) was considered a replicate and weighted according to its size (= number of plots within that particular population).

Further, we tested if the basic habitat characteristics differed between the two continents and ranges. Using a simple categorization of habitats (grasslands, forest edges, scrub, riparian habitats, arid habitats, moist to wet habitats, ruderal and synanthropic habitats, and abandoned grasslands), we created glm models with (1) continent and (2) range as predictors and counts of species in habitat categories as a response variable.

The strength of competition between species can also depend on their phylogenetic relatedness, with more intense competition expected among closely related rather than unrelated species (Procheş *et al.*, 2008). For this reason, we counted the numbers of species that were (1) confamilial, (2) congeneric and (3) unrelated to the selected dominants in their native and invaded ranges and tested if the representation of related and unrelated species differed between the ranges.

RESULTS

The response of the community species richness to the dominant species cover differed between their native and invaded ranges for *Agrostis capillaris*, *Bromus tectorum*, *Cirsium arvense* and marginally significantly also for *Lupinus polyphyllus*. In case of *Aster novi-belgii* and *Solidago canadensis*, no significant difference was detected in their relationship to species richness across the two ranges. *Agrostis capillaris*,

Bromus tectorum, *Cirsium arvense* and marginally significantly also *Lupinus polyphyllus* all suppressed the other species richness more in the invaded rather than native ranges.

Overall, the richness of native species in the plant community responded significantly more negatively to the dominant species cover in its invaded rather than native range, regardless of the identity of the dominant species (Table 4). In the invaded ranges, the negative response of species richness to the increasing dominant species cover was significantly stronger for European species invasive in North America compared with North American species invasive in Europe, as indicated by the significant three-way interaction between the dominant species cover and the terms 'range' (native, invaded) and 'continent' (North America, central Europe – Table 4).

For all species native to Europe and invasive in North America (*Agrostis capillaris*, *Bromus tectorum* and *Cirsium arvense*), the richness of native species in the invaded range decreased with increasing cover of the dominant (Table 2 and Fig. 1). In these dominant species, native range, only *Agrostis capillaris* suppressed the richness of native species, while no relationship between their cover and native species richness was found for *Bromus tectorum* and *Cirsium arvense*.

In the case of species invading from North America to Europe (*Aster novi-belgii*, *Lupinus polyphyllus* and *Solidago canadensis*), richness of native species decreased with increasing cover of *Aster novi-belgii* and *Lupinus polyphyllus* in the invaded range. However, species richness in the native North American range of these species also decreased with increasing cover, even though in the case of *Lupinus polyphyllus*, the negative relationship in the invaded range was only marginally significantly more pronounced compared with the native range (Table 3). On the contrary, species richness of the plant community dominated by *Solidago canadensis* decreased with increasing cover only in this species native range (Table 2). The cover of the other two species invading from North America to Europe (*Aster novi-belgii* and *Lupinus polyphyllus*) exhibits, in their native range, a polynomial (negative quadratic) rather than linear relationship to the richness of other species (Table 2 and Fig. 1).

Climatic variables, expressed as the PCO scores (Dupin *et al.*, 2011), related to species richness and differed between the two continents and between the ranges (Tables S1 and S2, respectively, in Appendix S1). The PCO scores representing the mean temperature and precipitation in the wet period were positively related to species richness, those representing precipitation in the dry period negatively (Table S1 in Appendix S1). The sites in Europe have higher PCO scores for the mean temperature and lower for precipitation in the wet period. Invaded ranges had a higher PCO score for precipitation both in the dry and wet period of the year (Table S2 in Appendix S1).

Basic habitat characteristics also differed between the continents and ranges (Table S3 in Appendix S1). North America, as well as the invaded ranges, had a higher representation of arid habitats, while Europe of ruderalized

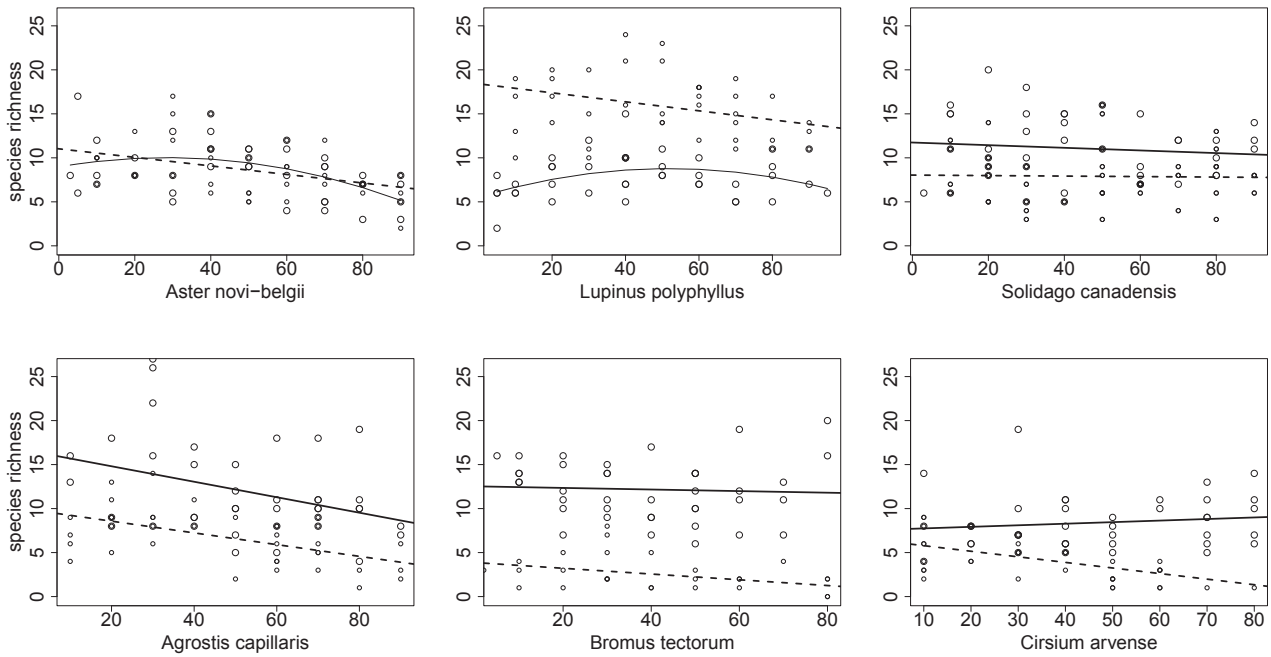


Figure 1 Relationships between the cover of species invading from North America to Europe (*Aster novi-belgii*, *Lupinus polyphyllus*, *Solidago canadensis*) and, vice versa, native to Europe and invading in North America (*Agrostis capillaris*, *Bromus tectorum*, *Cirsium arvense*), and native species richness. The full line represents this relationship in the dominant species native range and the dashed line in the invaded range. The figure shows general trends across populations and does not reflect the spatial clustering of the data, so the lines differ from the estimates in Tables 2 & 3.

habitats. In the native ranges, abandoned grasslands were more represented.

The representation of related species differed between ranges for none of the selected dominants but *Cirsium arvense*, where confamilials were over-represented in the invaded range ($P = 0.04$; Table S4 in Appendix S1). No disproportionality in the representation of congeners was found, but their numbers were generally low (Table S4 in Appendix S1).

DISCUSSION

All selected species that invade from Europe to North America (*Agrostis capillaris*, *Bromus tectorum* and *Cirsium arvense*) suppress the richness of native species in their invaded range. Although being a relatively slender plant, *Agrostis capillaris* forms dense stands and accumulates dead biomass over the years, which is a mechanism by which invasive species can prevent native species from reproducing (Larkin *et al.*, 2012). A strong community-level impact is reported from temperate South America for a related Eurasian grass *Agrostis stolonifera* (Gremmen *et al.*, 1998). A similar mechanism is in play for *Bromus tectorum*, an annual species that outcompetes native perennial grasses by accumulating dead biomass, preventing native perennial species from resprouting (Mack, 1989). Further, the accumulation of dead biomass is known to increase the frequency of fire events (Johnson *et al.*, 2011), which is a factor presumably favouring the invasive alien (Monty *et al.*, 2013). The invasion of *Bromus tectorum* is also very likely supported by its different phenology

compared with native grasses (Meyer *et al.*, 1997; Hardegreve *et al.*, 2010). Being a 'winter annual grass', *Bromus tectorum* germinates in the fall rather than in the spring, which makes it able to produce biomass earlier and therefore outcompete native species, which germinate in early spring (Beckstead *et al.*, 1996; Bykova & Sage, 2012). Interestingly, the dominance of *Agrostis capillaris* was found to suppress species richness even in its native range of central Europe; still, the negative response of species richness to the cover of *Agrostis capillaris* was more pronounced in this grass' invaded range. This indicates that when competing with *Agrostis capillaris*, European species are more successful compared with species native in North America. On the contrary, *Cirsium arvense* is a vigorous perennial, which is a strong competitor to native species of the tall grass prairies (Larson *et al.*, 2001). This distinctive dominant can cover large areas of a prairie, even though it tends to be most abundant in highly productive sites such as wet depressions or sites with a history of disturbance (Wilson & Pinno, 2012) or a regular fire regime.

Two North American species invading Europe (*Aster novi-belgii* and *Lupinus polyphyllus*) suppress species richness in the invaded central European range. However, the same is true for these species in their native range of the Atlantic Northeast and Pacific Northwest of the USA, respectively. Interestingly, species richness showed a negative quadratic rather than linear relationship to their cover in the native range. Contrary to that, the quadratic term for the data from the invaded range was not significant for both *Aster novi-belgii* and *Lupinus polyphyllus* (Fig. 1, Table 2). It is possible that the nature of the

response of species richness to the cover of these dominant species differs between the ranges. For example, species in the native North American range may be able to withstand a certain degree of these species dominance, even though they still cannot grow in really dense stands. This could result in a negative-quadratic shape of the relationship between the dominant's cover and richness of other native species.

For all selected species invading from Europe to North America (*Agrostis capillaris*, *Bromus tectorum* and *Cirsium arvense*), the response of species richness to the dominant species cover differed between the ranges, with the species in the invaded range (North America) being more likely eliminated from communities with a high cover of these species of European origin. Of North American species invading central Europe, a marginally significant difference between native and invaded ranges in the relationship of its cover to species richness was revealed for *Lupinus polyphyllus*.

Does this pattern suggest that European invaders in North America have a stronger community-level impact than North American invaders in Europe? The model, where the species identity was considered a random factor, suggests so. Moreover, the successful performance of European species as invaders elsewhere has been described before (Stohlgren *et al.*, 2011) and explained upon evolutionary background, in particular by a long-lasting association with humans and human-impacted landscape (di Castri, 1989; Sax & Brown, 2000; Seastedt & Pyšek, 2011). However, although our dataset covers a large scale of environmental gradients, especially from moist to dry, it is based on six dominant species only, and its general validity needs to be tested on a wider sample, ideally also for other regions and life-forms of the dominant species. The selection of species for this study was limited not only by that the whole sampling needed to be done by a single researcher but mainly by the requirement that selected species reach a comparable degree of dominance and occupy comparable habitats in both ranges.

When interpreting the results, it needs to be considered that the gradient of the dominant species cover is likely to be confounded with other factors, such as total biomass or productivity. Productive communities tend to host distinctive dominants. For this reason, it may be simplifying to interpret the relationship between a species cover, as a measure of its dominance, and species richness as the dominant species impact on the invaded community. However, the diversity of native species found in heavily invaded or strongly dominated communities likely reflects some large-scale effect. The measure of this effect is the number of species within local species pools that are able to exist under a high cover of the dominant species. Therefore, the negative response of species richness to the prevailing species dominance reflects the ability of local or regional species pools to provide species capable of existing under a high cover of the dominant native or invasive species. In other words, even though the dominance is likely caused by factors such as high resource availability and low stress levels, species richness is reduced because of the competitive effects of dominant species rather than because of the above factors –

high productivity may be the ultimate cause of diversity loss, while the dominant species competitive effect is the proximate cause. Therefore, the observed relationships between the dominant species covers and species richness are probably an aspect of the productivity–diversity relationship. However, the described large-scale effects show that the productivity–diversity relationships differ between the ranges and continents, most likely due to different competitive abilities of the local native species.

Possible differences between habitats in the native and invaded ranges represent another caveat. The target dominant species were sampled in a relatively broad range of open habitats, from wet and ruderalized forest and grassland edges to dry grasslands. Although attention was paid to sample comparable habitats in both ranges for each target dominant species, arid habitats were more represented in North America than in central Europe and in the invaded ranges compared with native ranges. Although less intensive competition has been suggested for dry habitats, where even facilitative interspecific relationships may occur (Campbell & Grime, 1992; Grime, 2007), our results show the opposite – species are more likely eliminated from communities in dry habitats in the North America and in the invaded rather than native range. As expected, central Europe shows a higher representation of ruderalized habitats, even though a degree of disturbance has been observed in both ranges. Similarly to arid habitats, a level of competition can be presumed to be lower in disturbed habitats (Belsky, 1992; Campbell & Grime, 1992; Mason *et al.*, 2011). Therefore, the lower level of disturbances in North America may lead to more intense competition between species, contrary to higher stress levels due to aridity.

The results may be further impacted by large-scale environmental factors, confounded with the transcontinental arrangement or with the delimitation of native and invaded ranges. For example, the sites in Europe exhibited higher values of the scores representing mean annual temperatures and lower values of the scores representing precipitation during the wet period of the year. Both these climatic variables were positively related to species richness, while the one representing precipitation in the dry period was negatively related to the species richness. This pattern suggests that sites in Europe could possess more species due to higher mean temperatures or lower seasonality in precipitation. Further, a higher species richness may indicate a higher degree of biotic resistance of central European communities to invasive alien species, as described by Levine *et al.* (2004). However, the fact that central European communities may be less invasible due to biotic resistance does not say anything about the impacts of the target species with the same degree of dominance between the continents and ranges. Finally, although the impact of dominant species can be affected by phylogenetic relatedness (e.g. Procheş *et al.*, 2008), the effects we found within our datasets were minor and limited to one species only, *C. arvense*, and did not suggest a systematic effect.

For all these reasons, the conclusions based on this dataset need to be conservative. We show that (1) a species'

dominance can limit community diversity also in its native range, as demonstrated by the effects found for *Agrostis capillaris*, *Aster novi-belgii*, *Solidago canadensis* and *Lupinus polyphyllus*. This is in concordance with the diversity–productivity relationship (Cox, 2004; Steiner & Leibold, 2004; Guo *et al.*, 2006; Guo, 2007), which assumes that highly productive sites tend to be overgrown by dominants that limit the occurrence of less vigorous species. (2) Even with the low number of target dominant species, the selected dominant species impact species richness more in their invaded rather than native ranges. The mechanisms associated with the long-term coexistence and filtering of species capable of competing with the dominants are among the likely causes of this phenomenon (Cox, 2004). These results contradict the suggestion that the origin of species does not matter (Thompson & Davis, 2011), an approach that does not take into account large-scale evolutionary patterns (Sax & Brown, 2000; Hulme *et al.*, 2011; Fridley, 2013). Our results show that, at least in case of the dominant species studied here, alien status is consistently associated with traits resulting in high vigour and more pronounced effects on species richness compared with native dominants. For example, the alien status can be associated with the opposing responses of species to grazing and increasing trophic levels, as demonstrated by Seabloom *et al.* (2015) on the grassland species. (3) The selected European invaders in North America have stronger negative impacts on species richness compared with selected North American invaders in Europe. Large-scale evolutionary patterns may be associated with this difference, such as that European species have been confronted with human-shaped environments for a long time or that they have been able to migrate over long distances from west to east and vice versa (di Castri, 1989; Sax & Brown, 2000; Seastedt & Pyšek, 2011; Fridley, 2013). These factors may have contributed to the competitive vigour of species native to Europe and, on the contrary, to the relative evolutionary naivety of North American species (Callaway *et al.*, 2008).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional analyses of potentially confounding factors.

BIOSKETCHS

The authors are members of a research team led by **Petr Pyšek**, with long-term interest in biological invasions, focusing on theoretical aspects of invasion process, species invasiveness, habitat invasibility, impacts of invasive plants, dynamics of alien species spread and macroecological patterns of biological invasions. The research of **Martin Hejda** and **Kateřina Štajerová** focuses on biogeographical transcontinental comparisons of community ecology and impacts of plant invasions.

Author contributions: M.H., K.S. and P.P. conceived the idea and sampling design; M.H. collected and analysed the data; M.H., K.S. and P.P. wrote the article.

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