

## Impact of invasive and native dominants on species richness and diversity of plant communities

Vliv invazních a původních dominant na druhovou bohatost a diverzitu rostlinných společenstev

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Hejda M., Sádlo J., Kutlvašr J., Petřík P., Vítková M., Vojík M., Pyšek P. & Pergl J. (2021) Impact of invasive and native dominants on species richness and diversity of plant communities. – Preslia 93: 181–201.

Invasive alien plants are known to reduce the diversity of recipient communities. However, there is an ongoing debate on whether or not native dominant species have similar effects. To answer this question, we compared herbaceous dominant species of plant communities in central Europe, 10 of which were native and nine alien to this region. We sampled 5–16 populations per species, selected to reflect a gradient from a low to a high cover of the dominant species studied and include a range of typical habitats. To reveal the possible effect of scale, we sampled the vegetation in 4 × 4 m (large scale) and 1 × 1 m (small scale) plots. All vascular plant species and their percentage covers were recorded in each plot. LMM regressions models were used to relate the dominant species' cover to the richness and diversity of the plant community and ANCOVAs to test for differences between the impacts of native vs. invasive dominants. On the large scale, 17 dominants (nine native and eight invasive) significantly reduced community species richness, and seven (four native and three alien) decreased species diversity measured using the Shannon H' index. *Reynoutria xbohemica*, *Calamagrostis epigejos* and *Phalaris arundinacea* had the strongest negative impact on species richness, while *Reynoutria xbohemica*, *Phalaris arundinacea* and *Urtica dioica* had the strongest impact on species diversity H'; the results at the small scale were very similar. No significant differences in impacts were detected with regard to the origin of the dominant species when all 19 dominants were included in one model. Further, we used indirect gradient ordination analysis (DCA) to identify pairs of native and invasive dominants that grow in similar habitats and, thus, their impacts can be compared and tested for the effect of origin (native vs. alien). This procedure yielded 27 pairs in total, as some dominants occur in more than one type of habitat and could, therefore, be coupled with more than one species from the other group. At the large scale, native dominants had stronger impacts on species richness in three cases (*Calamagrostis epigejos*, *Cirsium oleraceum* and *Phalaris arundinacea*) and invasive dominants in two (*Aster novi-belgii* agg. and *Rumex alpinus*), making up 11.1% and 7.4% of the total number of pairs examined, respectively. Only the invasive dominants (*Reynoutria xbohemica*, *Rumex alpinus*) had stronger impacts on species diversity H', in four pairwise comparisons (14.8%). The differences were not significant at the small scale in all but one comparison. The results show that both native and invasive dominants can reduce the diversity of vegetation. To conserve biodiversity, measures should be adopted to mitigate not only the impacts of invasive species but also

those of native dominants, spreading in the current landscape; this would be best achieved by promoting traditional management and land-use.

Keywords: dominance, impact, invasive alien species, land-use change, native species, origin, plant community, species diversity, species richness

## Introduction

Invasive alien plants are generally recognized as a threat to global diversity, and this is supported by robust data and syntheses (e.g. McGeoch et al. 2010, Vilà et al. 2011, Pyšek et al. 2020b). These effects are manifest across multiple scales, with plant communities being the one where ecological processes occur, which determine the impacts of invasion that result from interactions between native and alien species (Divíšek et al. 2018). By reducing species richness, many invasions result in depauperated vegetation, where a limited subset of resistant native species persist. It has been shown for some invaders, that the species richness prior to invasion is reduced by as much as 90% (Hejda et al. 2009).

However, a debate started in the last decades about whether the impacts of alien species on biodiversity and ecosystem functioning are similar to those of widespread, dominant native species (e.g. Aynsley & Rasmussen 2005, Davis et al. 2011, Carey et al. 2012, but see Simberloff et al. 2011). This is rarely rigorously tested, but the few studies that address this issue report contrary evidence (e.g. Paolucci et al. 2013, Buckley & Catford 2016, Hejda et al. 2017). For plants, established alien species were shown to be 40 times more likely problematic for local ecosystems in the USA than are native species (Simberloff et al. 2012). Several studies documented the community-level impacts of the same species in its native and invaded ranges (Hejda 2013, Hejda et al. 2017, 2019), showing that in the native range they are generally milder than in the invaded range. Other studies compare the impacts of native and invasive dominants, illustrating that the latter had stronger impacts (Hejda et al. 2017, 2019). The differences in the impacts of native vs. invasive dominants or between the native and invaded ranges can be generally attributed to different evolutionary histories, i.e. to the ‘evolutionary naivety’ of species in the invaded ranges when confronted with dominant invasive species.

Buckley & Catford (2016) outline how origin effects can cascade through and generate ecological impacts at population, community and ecosystem levels. They argue that rejecting the role of biogeographic origin as an explanation for ecological impacts and not taking it into account in ecosystem management is overly simplistic. However, they conclude that species origin on its own should not be used as a shortcut for management decisions (Buckley & Catford 2016). Another line of robust evidence that origin matters comes from the IUCN Red List database (IUCN 2017). An analysis of data on global extinctions shows that alien species contributed to 25% of plant extinctions and 33% of terrestrial and freshwater animal extinctions; these figures are an order of magnitude higher than for native species, which are implicated in fewer than 5% and 3% of plant and animal extinctions, respectively (Blackburn et al. 2019). Still, there is an ongoing debate on whether and how the impacts of invasive aliens differ from those of expanding native dominants (Richardson & Ricciardi 2013, Simberloff et al. 2013, Simberloff & Vitule 2014, Hulme et al. 2015, Thomas & Palmer 2015, Anderson et al. 2019).

In non-forest habitats in central Europe, the expansions of native dominant species are one of the striking aspects of the landscape changes since the second half of the 20th century (Kopecký 1984, Prach & Wade 1992), accelerating markedly in the last few decades. The expanding natives usually originate from disturbed and/or eutrophic habitats, such as abandoned fields and meadows or nitrophilous fringes. This corresponds to the fact that many European species that are successful invaders worldwide originate from disturbed and eutrophic habitats in their native range (Hejda et al. 2015). Many such species, so-called ‘apophytes’ (a term used for native species occurring in secondary habitats, see Holub & Jirásek 1967), are rapidly growing native nitrophilous dominants, utilizing available resources in the same way as is suggested for invaders (Davis et al. 2000, Blumenthal 2006, Blumenthal et al. 2009, Dostál et al. 2013). Some native nitrophilous dominants are remarkably aggressive, rapidly spreading and can impact vegetation in a similar way to invasive species.

Despite the intensive debate, studies comparing the community-level impacts of a sufficient number of native versus invasive dominants that would allow for broader generalization are lacking, even though some studies explore the community-level impacts of native species (e.g. Pivello et al. 2017). Yet, the knowledge of how both groups compare in terms of impact on resident vegetation is important also for managers of nature conservation, where the issue of prioritizing budget and management actions is crucial for decision-making (Hulme et al. 2014, Pyšek et al. 2013, Foxcroft et al. 2017).

To obtain insights into the above-described phenomena, we conducted a field study comparing the community-level impacts of a number of native and invasive species that are dominant in central-European non-forest vegetation. This enabled us to address the following questions: (i) Does the impact of native dominant plant species on species richness and diversity of the plant communities in which they grow differ from that of invasive aliens? (ii) Which native and invasive dominants exert the strongest and the weakest impact? (iii) For the same habitat, represented by a similar type of plant community, do invasive aliens exert stronger impacts than ecologically analogous native dominants? (iv) Do the impacts of both invasive and native dominants differ with respect to spatial scale, represented by  $4 \times 4$  m plots, and  $1 \times 1$  m plots nested within the larger ones?

## Methods

### *Sampling design*

We selected 10 expansive native (sensu Prach & Wade 1992) and nine invasive alien (sensu Blackburn et al. 2011) dominant plant species frequently occurring in the Czech Republic. They included a range of life forms (with the majority of 16 polycarpic perennials, seven of them rhizomatous, and one each of monocarpic perennial, annual and shrub) growing in habitats classified as various types of grassland and riparian vegetation (Table 1). Among the native dominants, two species are classified as archaeophytes (*Cirsium arvense*, *Tanacetum vulgare*; Pyšek et al. 2012a), i.e. not native to the region studied but introduced a long time ago; their residence time in central Europe is at least ~6500 yrs (Scheepens 2007, Pokorná et al. 2018). Due to their long-term presence, they can be considered as fully integrated into local vegetation and a permanent and stable component of the flora, not exhibiting rapid changes in occurrence or abundance.

Table 1. – The native (expansive) and invasive dominant species included in this study, with information on their life form (pp – polycarpic perennial, mp – monocarpic perennial, a – annual, sh – shrub; nc – non-clonal, s – stoloniferous, t – tufted), habitats in which they were sampled, and the continent of origin for alien species. The description of habitats where sampling was made is provided; forests, shrubland, recently and/or heavily disturbed ruderal sites as well as recently abandoned cultures, managed (mown) and trampled sites were excluded.

Dominant species	Life form	Habitat	Status
<i>Aster novi-belgii</i> agg.	pp-s	urban sites (5–10 yrs of succession)	invasive (N America)
<i>Calamagrostis epigejos</i>	pp-s	urban sites, post-meadow sites	native
<i>Cirsium arvense</i>	pp-s	urban sites, post-meadow sites	invasive archaeophyte (Europe, Asia)
<i>Cirsium heterophyllum</i>	pp-t	post-meadow sites: mountain belt	native
<i>Cirsium oleraceum</i>	pp-t	post-meadow sites, riverine sites	native
<i>Filipendula ulmaria</i>	pp-t	post-meadow sites	native
<i>Heracleum mantegazzianum</i>	mp-nc	post-meadow sites	invasive (C Asia)
<i>Impatiens glandulifera</i>	a-nc	riverine sites	invasive (C Asia)
<i>Lupinus polyphyllus</i>	pp-nc	post-meadow sites	invasive (N America)
<i>Petasites hybridus</i>	pp-t	post-meadow sites, riverine sites	native
<i>Phalaris arundinacea</i>	pp-s	post-meadow sites, riverine sites	native
<i>Reynoutria japonica</i>	pp-s	urban, post-meadow and riverine sites	invasive (E Asia)
<i>Reynoutria ×bohemica</i>	pp-s	urban, post-meadow and riverine sites	invasive (E Asia)
<i>Rubus idaeus</i>	sh-s	post-meadow sites	native
<i>Rumex alpinus</i>	pp-t	post-meadow sites: mountain belt	invasive (Europe)
<i>Solidago canadensis</i>	pp-s	urban sites	invasive (N America)
<i>Tanacetum vulgare</i>	pp-t	urban sites (5–10 yrs of succession)	invasive archaeophyte (Europe)
<i>Telekia speciosa</i>	pp-t	post-meadow and riverine sites	invasive (Europe)
<i>Urtica dioica</i>	pp-s	urban, post-meadow and riverine sites	native

For each dominant species, we identified sites harbouring populations large enough to facilitate the location of sampling plots and the use of their various covers as a measure of their dominance. We chose only those sites where the vegetation was, inferring from the character of the site, likely to be driven by competition rather than by disturbance or stress. We therefore avoided (i) early successional stages following a major disturbance; (ii) permanently disturbed sites; and (iii) sites previously used for cultivation and recently abandoned. There were 5–16 sites (populations) per species, depending on the availability of sites meeting the sampling criteria; the sites were distributed in various parts of the Czech Republic (see Electronic Appendix 1 for their locations). Ideally, it was possible to sample two plots at each site with the dominant-species cover exceeding 50% and two plots with 25–50% cover; the other two plots with less than 25% cover of the target dominant species served as controls. These control plots did not contain any other dominant species, native or alien, with a cover exceeding 25%.

The sampling was carried out in plots of two sizes to test for the effect of spatial scale on impact: 4 × 4 m (further referred to as ‘large plots’), within which we placed smaller subplots 1 × 1 m (‘small plots’). In some cases, it was not possible to locate the small plot within the large one; therefore, the numbers of plots sampled per species differ slightly (Table 3). All vascular plant species were recorded in each plot, and their percentage covers were estimated visually. The field sampling was carried out during the vegetation seasons (June–September) of 2017–2019.

### Statistical analyses

The relations between the dominant species' cover and community species richness and diversity were evaluated using linear mixed-effect regression models (LMM), where the identity of populations represented the random effect (Zuur et al. 2011, Pekár & Brabec 2012). In analyses with all dominant species included in the model, the dominant species' identity was set as another random effect ('dominant'), with the 'population' nested in 'dominant'. The differences between the impacts of native versus invasive dominants were tested using the LMM analyses of covariance. The dominant species' cover was a continuous predictor variable, and the native/alien status of the dominant species was a factor predictor variable. The cover  $\times$  dominant species' origin interaction was of most interest, as it showed whether the impact of the native dominants differed from that of the invasive dominants. The covers of dominants, expressed on a percentage scale, were arcsin transformed prior to both LMM regressions and analyses of covariance. All statistical analyses were carried out in R software (R Development Core Team 2013). All LMM models were created using the NLME package (Pinheiro et al. 2021). The numbers of species and Shannon diversity indices  $H'$  (Magurran 1988), calculated without the target dominant species, were used as response variables.

We used the slope/intercept ratios of LMM regressions to express the magnitude of impacts of individual dominants on species richness and Shannon diversity  $H'$ . This ratio shows the proportion of species disappearing due to the increasing cover of the dominant species, therefore accounting for the initially different richness and diversity of different types of communities.

Indirect gradient ordination analysis (detrended correspondence analysis, DCA; Lepš & Šmilauer 2014) was used to identify the pairs of native/invasive dominants that are likely to occur in the same or similar habitats. Individual plots were the replicates, the covers of recorded species were used as the response variables, and selected dominant species' identities were projected onto the ordination plot post-hoc as 'supplementary environmental variables.' Only plots with  $\leq 25\%$  dominant species' cover were used, as plots with a low cover of dominants were considered as a control in relation to the plots with a high cover of that particular dominant within each locality. The distances between the centroids of individual native and invasive dominant species were calculated as

$$X = \sqrt{(n_{1st} - i_{1st})^2 + (n_{2nd} - i_{2nd})^2}$$

where  $n_{1st}$  and  $i_{1st}$  are the 1<sup>st</sup> axis scores of the native and invasive dominant, respectively, and  $n_{2nd}$  and  $i_{2nd}$  are the 2<sup>nd</sup> axis scores.

The ordination distances were counted for all possible pairs of native and invasive dominant species. For each invasive dominant species, three pairs with native dominants were identified as those to which the invasive species showed the smallest ordination distance. This yielded 27 pairs of native–invasive dominants for the large plot scale (4  $\times$  4 m) and 24 pairs for the small scale (1  $\times$  1 m) (Fig.1). The differences in the impacts of invasive and native dominants within pairs were tested using the LMM ANCOVA.

The species ranking by their impact on community species richness and diversity  $H'$  was tested by a linear model with offset (Crawley 2007). Species showing different ranks were identified by Cook's distances.

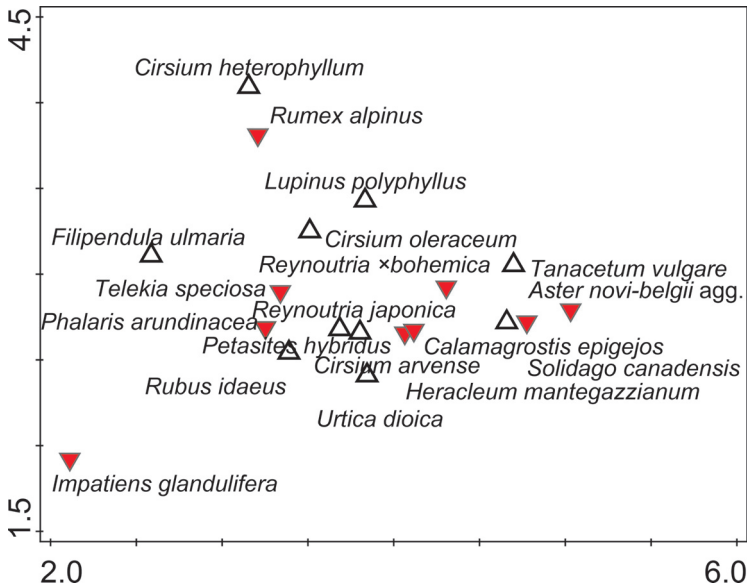


Fig. 1. – Ordination plot from the indirect gradient ordination analysis (DCA), used to identify pairs of  $\Delta$  native and  $\blacktriangledown$  invasive dominants spreading in the same or similar habitats (see Table 4). The identities of dominants are projected onto the plot as supplementary variables.

## Results

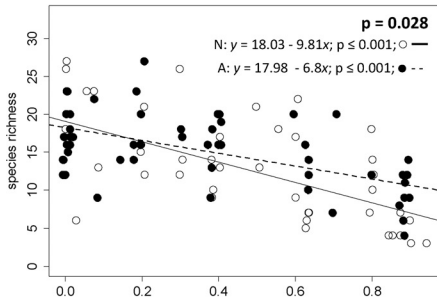
### *Relation between the cover of dominant species and community species richness and diversity*

At the large scale, 17 dominants (9 native and 8 invasive, representing 90% and 89% of the total numbers of species studied, respectively) had a significant impact on the species richness of plant communities, but only 7 (4 natives and 3 invasive species, i.e. 40% and 33%, respectively) were found to reduce species diversity  $H'$ . At the small scale, 16 dominant species (9 native and 7 invasive, i.e., 90% and 78%, respectively) had an impact on species richness. The number of species with significant impact on species diversity  $H'$  was 8 (5 natives and 3 invasive, i.e. 50% and 33% of the total number of species studied) (Table 2). Significant negative quadratic terms were identified in the LMM regression models for *Impatiens glandulifera* and *Rumex alpinus*, but only at the large scale of  $4 \times 4$  m (Fig. 2).

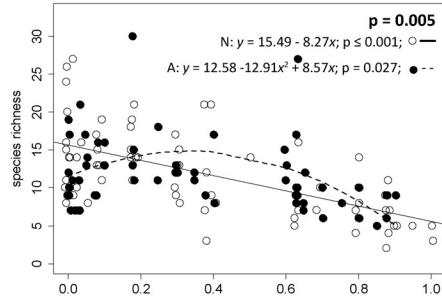
The impacts recorded in the large vs. small plots differed significantly for species richness ( $P < 0.001$ ), but only marginally significantly for species diversity  $H'$  ( $P = 0.055$ ). However, when comparing the slope/intercept ratios, expressing the magnitude of impacts independent of the initial species richness or diversity, the difference was significant only for species diversity  $H'$  ( $P < 0.001$ ), showing a more negative impact at the small-scale of  $1 \times 1$  m (Electronic Appendix 2).

Fig. 2. – The relationships between species richness, Shannon diversity  $H'$  and the cover of native (N; full line, empty circles) vs. invasive dominants (A; dashed line, black circles). Only pairs with significant differences in their impacts on either species richness or species diversity  $H'$  are shown. The relationships are based on the large plots ( $4 \times 4$  m), except for the pair *P. hybridus* – *L. polyphyllus* for which the relationship is based on small plots ( $1 \times 1$  m).  $\blacktriangleright$

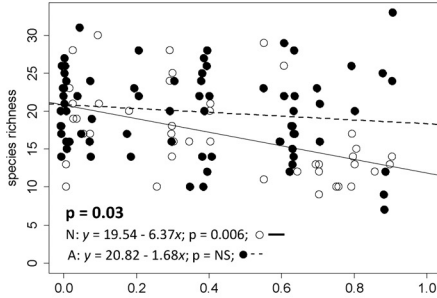
*C. epigejos* (N) – *A. novi-belgii* agg. (A)



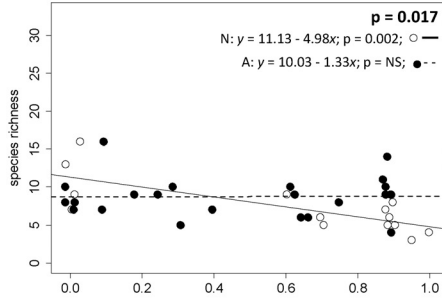
*P. arundinacea* (N) – *I. glandulifera* (A)



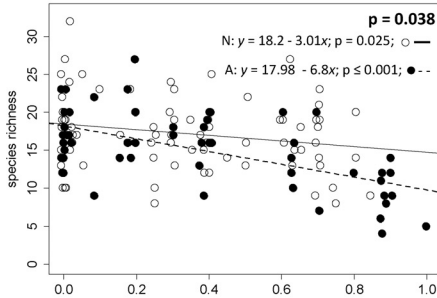
*C. oleraceum* (N) – *L. polyphyllus* (A)



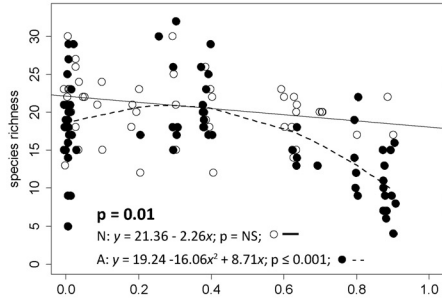
*P. hybridus* (N) – *L. polyphyllus* (A) (1×1 m)



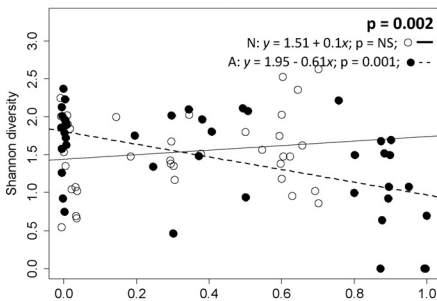
*T. vulgare* (N) – *A. novi-belgii* agg. (A)



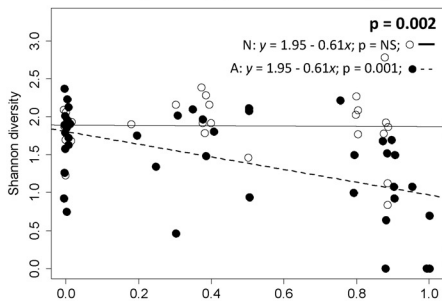
*C. heterophyllum* (N) – *R. alpinus* (A)



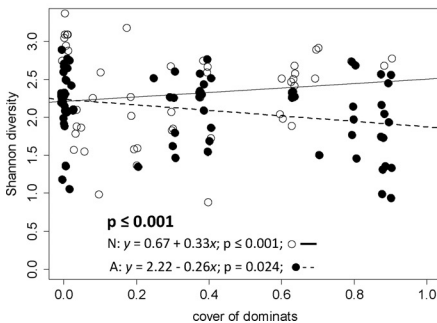
*C. arvensis* (N) – *R. xbohemica* (A)



*P. hybridus* (N) – *R. xbohemica* (A)



*C. heterophyllum* (N) – *R. alpinus* (A)



*C. oleraceum* (N) – *R. alpinus* (A)

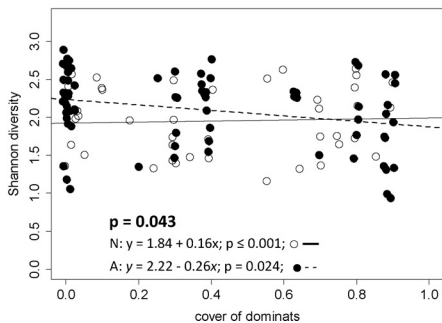


Table 2. – The numbers of native and invasive dominant species (out of 10 and nine included in the study, respectively) with significant and non-significant (NS) impacts on species richness/Shannon diversity  $H'$ . The difference in impact indicates the numbers of native–invasive pairs, in which one of the species had a significantly greater impact on species richness/ $H'$  than the other. The total number of pairs was 27 for the large scale ( $4 \times 4$  m plots), and 24 for the small scale ( $1 \times 1$  m plots).

Scale	Significant impacts		Non-significant impact		Difference in impact		
	Native	Invasive	Native	Invasive	Native > Alien	Alien > Native	NS
Large	9/4	8/3	1/6	1/6	3/0	2/4	22/23
Small	9/5	7/3	1/5	1/5	1/0	0/0	23/24

### *Dominants with a high versus low impact on species richness and diversity*

At the large-plot scale (Fig. 3, Electronic Appendix 2), *Reynoutria xbohemica*, *Calamagrostis epigejos* and *Phalaris arundinacea* had the most pronounced negative impacts on community species richness (measured simply by the numbers of species in the respective plots, these dominant species reduced the richness in their high-cover plots to 39%, 48% and 50%, respectively, of that in low-cover plots; Table 3). *Reynoutria xbohemica*, *Phalaris arundinacea* and *Urtica dioica* had the strongest negative impact on species diversity  $H'$ . *Cirsium heterophyllum*, *Lupinus polyphyllus* and *Tanacetum vulgare* had the least impact on both species' richness and diversity  $H'$  (Electronic Appendix 2; see also Table 3 for the percentage reduction of  $H'$  in plots with a high cover of the dominant species).

At the small-plot scale, *Reynoutria xbohemica*, *Urtica dioica* and *Phalaris arundinacea* had the strongest impact (with 27%, 46% and 58% of species present in low-cover plots persisting in high-cover plots), while *Lupinus polyphyllus*, *Tanacetum vulgare* and *Rumex alpinus* had the weakest impact on species richness (reducing it to 75–94% only). Species diversity  $H'$  at this scale was most strongly impacted by *Reynoutria xbohemica*, *Rumex alpinus* and *Urtica dioica*, whereas *Cirsium heterophyllum*, *Tanacetum vulgare* and *Lupinus polyphyllus* had the smallest impact (Table 3, Fig. 3, Electronic Appendix 2).

At the small scale, the ranking of dominant species by impact marginally significantly differed between species richness and diversity  $H'$  ( $P = 0.054$ ). In particular, the invasive dominant *Rumex alpinus* had the second strongest impact on species diversity  $H'$  at the small-plot scale but the third lowest impact on species richness (Fig. 3, Electronic Appendix 2).

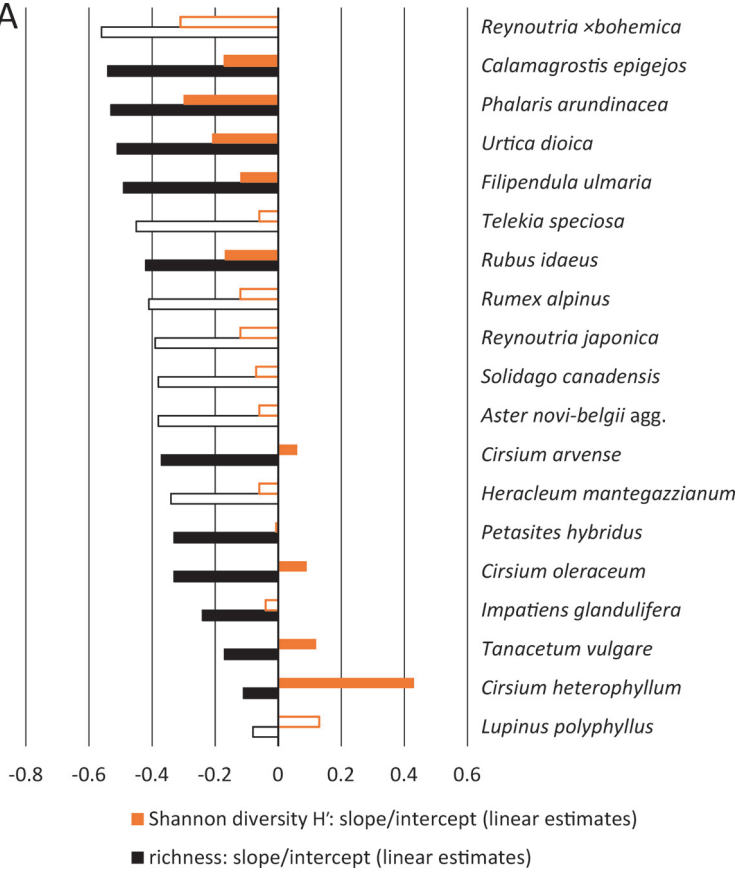
### *Differences in impacts of invasive and native dominants*

No differences in impacts on species richness and diversity  $H'$  were detected in a model with native and invasive dominants merged at the large scale ( $P = 0.234$  for species richness and  $P = 0.748$  for species diversity  $H'$ ). However, native dominants had a slightly greater negative impact on species richness at the small scale ( $P = 0.049$ ). Further, the triple interactions between the dominant species cover, its' origin (native or invasive) and plot

Fig. 3. – The dominant species included in the study ranked according to their impact on species richness and diversity  $H'$ , as recorded for (A) large plots ( $4 \times 4$  m) and (B) small plots ( $1 \times 1$  m). The magnitude of impact is expressed as the ratio of slope/intercept from the LMM regressions on the relationship between the cover of the dominants and community species richness and diversity  $H'$ . The significance levels and details on values of species richness  $S$  and diversity  $H'$  are shown in Electronic Appendix 2. Native dominants are indicated by solid bars, invasive dominants by empty bars. ►



A



B

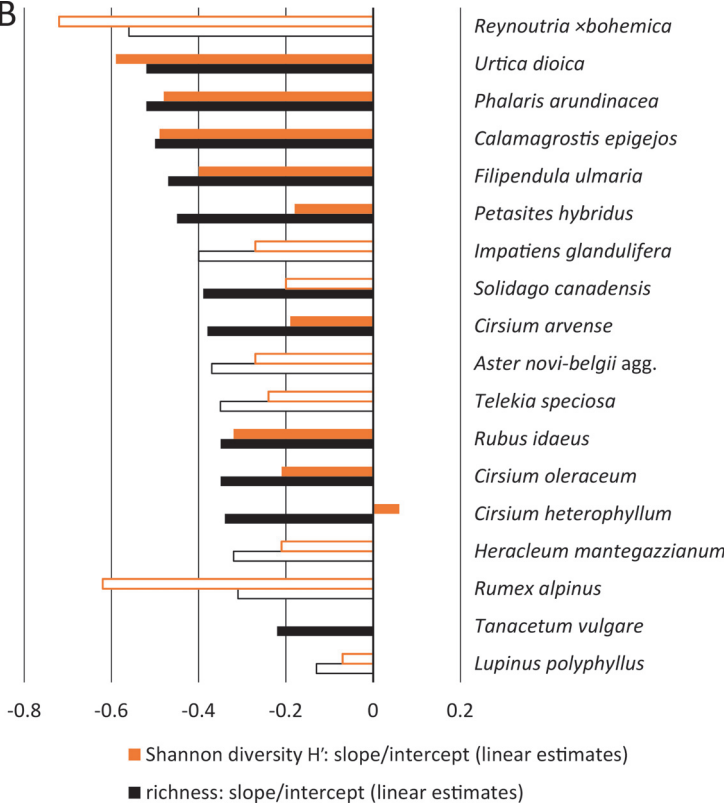


Table 3. – The native (expansive) and invasive dominant species included in this study, with information on species richness and diversity (mean  $\pm$  S.D.) in plots with low, medium and high cover of each dominant, as recorded in (A) large,  $4 \times 4$  m, and (B) small,  $1 \times 1$  m plots. N – number of plots sampled, S – species number,  $H'$  – Shannon index of species diversity. Low cover of the dominant species: 0–25%; medium cover: 26–50%; high cover: 51–100%. Also shown is the proportional reduction or increase in S and  $H'$  due to invasion, expressed as the ratio of species numbers and diversity between plots with high and low dominant species covers. Note that for *Reynoutria japonica*, data for small scale are not available, for *Petasites hybridus* they are not available for medium cover, and for *Cirsium heterophyllum*, only one small plot ( $1 \times 1$  m) was sampled for its low cover (0–25%).

Dominant species	N	Low cover		Medium cover		High cover		High/low cover	
		S	$H'$	S	$H'$	S	$H'$	S	$H'$
<b>A. Large scale</b>									
<i>Aster novi-belgii</i> agg.	9	17.3 $\pm$ 4.2	1.9 $\pm$ 0.4	16.5 $\pm$ 3.1	1.9 $\pm$ 0.3	11.2 $\pm$ 4.4	1.9 $\pm$ 0.6	0.65	0.97
<i>Calamagrostis epigejos</i>	11	17.7 $\pm$ 5.5	1.7 $\pm$ 0.5	14.7 $\pm$ 4.7	1.7 $\pm$ 0.4	8.9 $\pm$ 5.6	1.5 $\pm$ 0.6	0.50	0.87
<i>Cirsium arvense</i>	8	12.7 $\pm$ 6.8	1.5 $\pm$ 0.5	13.3 $\pm$ 4.5	1.5 $\pm$ 0.3	12.0 $\pm$ 4.8	1.6 $\pm$ 0.5	0.95	1.12
<i>Cirsium heterophyllum</i>	9	21.7 $\pm$ 5.1	2.3 $\pm$ 0.7	21.1 $\pm$ 5.1	2.1 $\pm$ 0.6	19.3 $\pm$ 2.6	2.5 $\pm$ 0.3	0.89	1.11
<i>Cirsium oleraceum</i>	9	19.8 $\pm$ 5.4	2.1 $\pm$ 0.4	18.8 $\pm$ 4.9	1.8 $\pm$ 0.4	14.1 $\pm$ 5.1	2.0 $\pm$ 0.5	0.71	0.97
<i>Filipendula ulmaria</i>	7	13.3 $\pm$ 5.0	1.7 $\pm$ 0.4	13.3 $\pm$ 3.9	1.7 $\pm$ 0.4	9.3 $\pm$ 3.1	1.5 $\pm$ 0.3	0.70	0.93
<i>Heracleum mantegazzianum</i>	8	11.0 $\pm$ 3.8	1.6 $\pm$ 0.3	6.8 $\pm$ 1.3	1.0 $\pm$ 0.3	5.1 $\pm$ 1.8	1.0 $\pm$ 0.5	0.46	0.61
<i>Impatiens glandulifera</i>	13	12.7 $\pm$ 5.1	1.6 $\pm$ 0.5	14.6 $\pm$ 7.9	1.8 $\pm$ 0.5	10.2 $\pm$ 4.6	1.5 $\pm$ 0.4	0.81	0.92
<i>Lupinus polyphyllus</i>	16	20.9 $\pm$ 4.5	2.3 $\pm$ 0.4	19.6 $\pm$ 5.9	2.1 $\pm$ 0.6	19.1 $\pm$ 6.1	2.4 $\pm$ 0.4	0.92	1.08
<i>Petasites hybridus</i>	5	16.3 $\pm$ 4.1	1.8 $\pm$ 0.2	16.3 $\pm$ 3.4	2.0 $\pm$ 0.3	11.3 $\pm$ 3.4	1.8 $\pm$ 0.5	0.69	1.02
<i>Phalaris arundinacea</i>	14	15.1 $\pm$ 4.8	1.9 $\pm$ 0.4	11.9 $\pm$ 4.8	1.5 $\pm$ 0.5	7.3 $\pm$ 3.2	1.3 $\pm$ 0.6	0.48	0.70
<i>Reynoutria japonica</i>	6	18.5 $\pm$ 8.8	1.7 $\pm$ 0.7	15 $\pm$ 12.1	1.6 $\pm$ 0.8	7.9 $\pm$ 4.6	1.4 $\pm$ 0.7	0.43	0.82
<i>Reynoutria <math>\times</math>bohemica</i>	8	13.4 $\pm$ 4.6	1.7 $\pm$ 0.4	12.8 $\pm$ 4.7	1.6 $\pm$ 0.5	5.3 $\pm$ 3.2	1.0 $\pm$ 0.7	0.39	0.60
<i>Rubus idaeus</i>	12	16.0 $\pm$ 6.3	1.9 $\pm$ 0.4	14.8 $\pm$ 2.9	1.7 $\pm$ 0.6	10.5 $\pm$ 4.6	1.6 $\pm$ 0.6	0.66	0.89
<i>Rumex alpinus</i>	12	18.4 $\pm$ 5.2	2.2 $\pm$ 0.5	21.3 $\pm$ 4.9	2.2 $\pm$ 0.4	12.0 $\pm$ 4.3	1.9 $\pm$ 0.5	0.65	0.89
<i>Solidago canadensis</i>	11	18.2 $\pm$ 6.2	2.0 $\pm$ 0.7	16.2 $\pm$ 4.4	2.0 $\pm$ 0.4	13.0 $\pm$ 4.9	1.9 $\pm$ 0.6	0.71	0.95
<i>Tanacetum vulgare</i>	15	18.6 $\pm$ 5.3	1.9 $\pm$ 0.4	16.0 $\pm$ 6.4	1.9 $\pm$ 0.4	16.1 $\pm$ 4.7	2.1 $\pm$ 0.5	0.87	1.08
<i>Telekia speciosa</i>	8	18.3 $\pm$ 5.6	1.9 $\pm$ 0.4	17.8 $\pm$ 5.4	2.1 $\pm$ 0.4	11.9 $\pm$ 3.5	1.8 $\pm$ 0.4	0.65	0.96
<i>Urtica dioica</i>	14	15.8 $\pm$ 5.9	1.9 $\pm$ 0.4	16.5 $\pm$ 3.1	1.7 $\pm$ 0.5	9.3 $\pm$ 3.2	1.5 $\pm$ 0.5	0.59	0.81
<b>B. Small scale</b>									
<i>Aster novi-belgii</i> agg.	7	7.3 $\pm$ 1.5	1.2 $\pm$ 0.3	7.5 $\pm$ 3.5	1.2 $\pm$ 0.3	4.8 $\pm$ 2.1	0.9 $\pm$ 0.6	0.66	0.74
<i>Calamagrostis epigejos</i>	9	8.7 $\pm$ 2.8	1.5 $\pm$ 0.2	8.8 $\pm$ 2.5	1.3 $\pm$ 0.4	4.8 $\pm$ 2.9	0.7 $\pm$ 0.5	0.56	0.50
<i>Cirsium arvense</i>	7	9.3 $\pm$ 2.4	1.5 $\pm$ 0.2	8.7 $\pm$ 3.4	1.4 $\pm$ 0.4	6.4 $\pm$ 1.7	1.2 $\pm$ 0.3	0.68	0.82
<i>Cirsium heterophyllum</i>	4	15.0	1.8	13.1 $\pm$ 6.9	1.8 $\pm$ 0.4	11.3 $\pm$ 3.2	2.0 $\pm$ 0.4	0.75	1.08
<i>Cirsium oleraceum</i>	9	10.5 $\pm$ 2.6	1.7 $\pm$ 0.4	10.3 $\pm$ 2.9	1.4 $\pm$ 0.5	6.9 $\pm$ 2.7	1.3 $\pm$ 0.4	0.65	0.76
<i>Filipendula ulmaria</i>	5	9.0 $\pm$ 1.8	1.5 $\pm$ 0.2	6.8 $\pm$ 1.3	1.0 $\pm$ 0.3	5.1 $\pm$ 1.8	1.0 $\pm$ 0.5	0.57	0.65
<i>Heracleum mantegazzianum</i>	7	8.6 $\pm$ 2.3	1.4 $\pm$ 0.3	8.9 $\pm$ 2.5	1.5 $\pm$ 0.4	5.4 $\pm$ 2.6	1.0 $\pm$ 0.6	0.62	0.75
<i>Impatiens glandulifera</i>	8	7.5 $\pm$ 1.8	1.2 $\pm$ 0.4	7.3 $\pm$ 2.0	1.4 $\pm$ 0.3	5.1 $\pm$ 1.9	0.9 $\pm$ 0.5	0.68	0.74
<i>Lupinus polyphyllus</i>	11	9.3 $\pm$ 2.9	1.6 $\pm$ 0.2	7.8 $\pm$ 1.9	1.4 $\pm$ 0.3	8.8 $\pm$ 2.5	1.6 $\pm$ 0.4	0.94	0.98
<i>Petasites hybridus</i>	4	11.3 $\pm$ 3.5	1.3 $\pm$ 0.2			5.8 $\pm$ 1.7	1.1 $\pm$ 0.4	0.52	0.83
<i>Phalaris arundinacea</i>	9	8.1 $\pm$ 2.8	1.3 $\pm$ 0.3	7.0 $\pm$ 1.7	1.2 $\pm$ 0.3	3.7 $\pm$ 1.7	0.7 $\pm$ 0.5	0.46	0.51
<i>Reynoutria <math>\times</math>bohemica</i>	4	6.3 $\pm$ 3.7	1.0 $\pm$ 0.5	5.0 $\pm$ 0.0	0.8 $\pm$ 0.3	1.7 $\pm$ 1.0	1.0 $\pm$ 0.1	0.27	0.03
<i>Rubus idaeus</i>	7	10.0 $\pm$ 1.5	1.5 $\pm$ 0.2	8.3 $\pm$ 3.4	0.7 $\pm$ 0.7	6.3 $\pm$ 2.2	1.0 $\pm$ 0.5	0.63	0.67
<i>Rumex alpinus</i>	9	9.5 $\pm$ 2.3	1.5 $\pm$ 0.4	6.0 $\pm$ 0.0	0.7 $\pm$ 0.2	6.2 $\pm$ 2.4	1.3 $\pm$ 0.5	0.65	0.90
<i>Solidago canadensis</i>	8	8.9 $\pm$ 3.1	1.4 $\pm$ 0.6	9.4 $\pm$ 3.0	1.3 $\pm$ 0.4	6.2 $\pm$ 2.4	1.2 $\pm$ 0.5	0.69	0.83
<i>Tanacetum vulgare</i>	15	9.6 $\pm$ 3.0	1.5 $\pm$ 0.3	7.4 $\pm$ 1.5	1.2 $\pm$ 0.4	7.7 $\pm$ 2.6	1.5 $\pm$ 0.5	0.80	0.98
<i>Telekia speciosa</i>	5	11.6 $\pm$ 3.7	1.7 $\pm$ 0.4	9.8 $\pm$ 3.4	1.5 $\pm$ 0.6	7.4 $\pm$ 3.4	1.3 $\pm$ 0.4	0.64	0.75
<i>Urtica dioica</i>	8	8.1 $\pm$ 2.0	1.4 $\pm$ 0.3	6.7 $\pm$ 1.5	1.1 $\pm$ 0.4	4.7 $\pm$ 2.0	0.8 $\pm$ 0.5	0.58	0.53

size were significant for both species richness and species diversity  $H'$  ( $P = 0.047$  and  $P = 0.007$ ), with the largest negative impacts recorded for native dominants in small plots.

At the large scale, native *Calamagrostis epigejos* had a greater impact on species richness than its invasive counterpart, *Aster novi-belgii* agg. ( $P = 0.028$ ), native *Phalaris arundinacea* had a greater impact than invasive *Impatiens glandulifera* ( $P = 0.005$ ), and native *Cirsium oleraceum* had a stronger impact than invasive *Lupinus polyphyllus* ( $P = 0.03$ ). On the contrary, the invasive *Aster novi-belgii* agg. and *Rumex alpinus* had stronger impacts on species richness than native *Tanacetum vulgare* and *Cirsium heterophyllum* ( $P = 0.038$  and  $P = 0.01$ , respectively). Concerning the impacts on species diversity  $H'$ , invasive *Reynoutria ×bohemica* and *Rumex alpinus* had stronger impacts than their native counterparts, *Cirsium arvense*, *Petasites hybridus*, *Cirsium heterophyllum* and *C. oleraceum* ( $P = 0.008$ ,  $P = 0.002$ ,  $P < 0.001$  and  $P = 0.043$ , respectively; Table 4).

The only significant difference between the impacts of native vs. invasive dominants recorded at the small scale was that of the native *Petasites hybridus* on species richness being stronger than that of the invasive *Lupinus polyphyllus* ( $P = 0.017$ ; Table 4).

Table 4. – Distances between pairs of native and invasive dominant species, as revealed by the ordination model (DCA). The native species are listed row-wise, invasive species column-wise, the pairs selected on the basis of the closest positions in the ordination space, reflecting the community species composition (see text for details) are indicated by shaded cells. Significant differences in impacts are indicated: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$  for species richness / Shannon diversity  $H'$  in large plots ( $4 \times 4$  m). The cases when the invasive dominant has a significantly stronger impact than the native dominant are marked by  $\uparrow$ . The only significant difference between the impacts of native vs. invasive dominants recorded at the small scale ( $1 \times 1$  m plots) was that of the native *Petasites hybridus* on species richness being stronger than that of the invasive *Lupinus polyphyllus* ( $P = 0.017$ ).

	<i>Aster novi-belgii</i> agg.	<i>Heracleum mantegazzianum</i>	<i>Impatiens glandulifera</i>	<i>Lupinus polyphyllus</i>	<i>Reynoutria japonica</i>	<i>Reynoutria ×bohemica</i>	<i>Rumex alpinus</i>	<i>Solidago canadensis</i>	<i>Telekia speciosa</i>
<i>Calamagrostis epigejos</i>	0.51*/	0.51	2.69	1.08	1.00	0.40	1.80	0.10	1.40
<i>Cirsium arvense</i>	1.10	0.10	2.10	0.76	0.40	0.22/↑**	1.42	0.71	0.81
<i>Cirsium heterophyllum</i>	2.39	1.64	2.42	0.85	1.39	1.63	0.2**/↑***	2.00	1.20
<i>Cirsium oleraceum</i>	1.87	0.94	1.84	0.45*/	0.58	0.98	0.63/↑*	1.46	0.41
<i>Filipendula ulmaria</i>	2.65	1.68	1.46	1.22	1.21	1.75	0.85	2.24	0.81
<i>Petasites hybridus</i>	1.40	0.40	1.84	0.70*/	0.10	0.51/↑**	1.25	1.00	0.51
<i>Phalaris arundinacea</i>	1.90	0.9	1.42**/	0.86	0.40	1.00	1.10	1.50	0.10
<i>Rubus idaeus</i>	1.81	0.82	1.39	0.98	0.36	0.95	1.32	1.43	0.32
<i>Tanacetum vulgare</i>	0.71↑*/	0.71	2.87	0.92	1.12	0.57	1.62	0.41	1.46
<i>Urtica dioica</i>	1.43	0.50	1.71	1.00	0.32	0.64	1.52	1.08	0.64

## Discussion

*The strength of impact is determined by species identity rather than its origin*

Our study provides robust evidence, based on a number of alien and native species that occur as dominants in plant communities, that both groups have comparable negative impacts on species richness and diversity. The impacts on species richness were more pronounced, with 17 out of the 19 species studied found to reduce community species richness as the

cover of the dominant species increased; species diversity measured as Shannon index  $H'$  was less affected, with a significant impact recorded for seven species, i.e. over a third of the total number. The likely reason for the observed differences in impacts on species richness vs. diversity may be that the dominant species reduce species richness without decreasing community evenness, since even a strongly dominated community may contain some persistent species with comparable relative abundances. Therefore, species richness is more reduced by the dominant species than species diversity. On the contrary, the dominants can reduce the evenness of a community without reducing its species richness. This can happen for example when the dominant species colonizes most of the space and therefore reduces the abundances of other species, but still leaves some space for them to persist (e.g. in a lower vegetation layer). In this case, the Shannon diversity would decrease but not species richness. In conclusion, species richness and Shannon diversity  $H'$  provide different views on the impacts of dominance on the recipient community.

In our study, we recorded the highest impact for two native perennial grasses (*Calamagrostis epigejos* and *Phalaris arundinacea*), alien stout herbs of the genus *Reynoutria* and a native apophyte, *Urtica dioica*. In accordance with previous research (Somodi et al. 2008, Pruchniewicz & Żołnierz 2016), the native *C. epigejos* had marked negative impacts on community richness and diversity at both spatial scales, reducing the number of species to about a half once it reached a cover of 50–100%. Such a decline in species richness at sites invaded by *C. epigejos* was attributed to light being the limiting factor rather than soil composition (Rebele 2000). However, both the shading effect of dense aboveground biomass (Somodi et al. 2008) and a thick layer of leaf litter (Pruchniewicz & Żołnierz 2016) were suggested as mechanisms leading to the suppression of other species. The spread of *C. epigejos* is a serious conservation problem, comparable to or locally even worse than the spread of many invasive aliens (Prach & Wade 1992). The relatively high impact of this aggressive native grass may also be associated with the fact that there are very few invasive grasses in central Europe, a life form that tends to have massive community-level impacts if it becomes invasive in a new region (di Castri 1989, Seastedt & Pyšek 2011, Hejda et al. 2017). Therefore, there is no invasive grass in central Europe whose impact could be compared to the impact of the dominant native grass, *C. epigejos*.

Another native grass, *Phalaris arundinacea*, is also a strong dominant, with a great suppressive effect on its community. Rapid spread, high tolerance to disturbance and ability to grow in soils of various properties and water regimes make both species successful under a wide range of ecological conditions (Rebele & Lehmann 2001, Lavergne & Molofsky 2004). Moreover, *P. arundinacea* is listed as an invasive alien species in wet prairies, stream-banks and wetlands of several parts of the United States (<https://www.invasiveplantatlas.org>) where it suppresses plant and insect diversity (Lavergne & Molofsky 2004, Spyreas et al. 2010) and causes biotic homogenization of wetland vegetation (Price et al. 2020). Indeed, our pairwise comparisons show that the expansion of these native species (*C. epigejos*, *P. arundinacea*) is a more serious problem for conserving the diversity than the invasions by aliens with similar habitat preferences such as *Aster novi-belgii* agg. or *Impatiens glandulifera*, respectively.

The invasive dominant *Reynoutria xbohemica* and, to some extent, also *Rumex alpinus* impose stronger impacts than native dominants with similar habitat preferences, such as *Cirsium arvense*, *Petasites hybridus*, *Cirsium heterophyllum* or *C. oleraceum*.

The relationship describing the impact of *R. alpinus* on species richness also contained a significant negative quadratic term, indicating that this invasive alien exerts disproportionately high impacts when it reaches a certain degree of dominance (~70–80% of cover, see Fig. 2). Delimat & Kiełtyk (2019) did not observe a considerable change in Shannon, Simpson and Pielou's diversity indices up to 30% of cover of *Rumex alpinus*, but further increase caused a steep decline in diversity. Similar to the native *C. epigejos*, *R. alpinus* spreads in vegetation of conservation concern (i.e. with relatively low human impact and low trophic levels). *Reynoutria* taxa are reported to negatively affect richness and biomass of not only plant but also invertebrate communities, reducing the quality of invaded ecosystems for other trophic levels (e.g. Gerber et al. 2008, Horáčková et al. 2014, Lavoie 2017). Unlike in Hejda et al. (2009), *R. xbohemica* in our present study showed a consistently higher impact on species richness and diversity than its congener, *R. japonica*. This was despite the taxonomic and ecological similarity of these two species. The observed differences in their impacts are possibly due to different habitat types and vegetation invaded by both taxa, i.e. semi-ruderal grasslands in *R. japonica* vs. riparian vegetation in *R. xbohemica*. Habitat type is an important factor codetermining the levels of invasion and impact (Chytrý et al. 2008a, Hejda et al. 2009), and riparian habitats in which the sample plots of *R. xbohemica* were located in our study are among the most prone to invasions by alien plants (Richardson et al. 2007, Chytrý et al. 2008b, Pyšek et al. 2010). Unfortunately, it is not possible to separate the effects of resident habitats from the effects of the individual dominant species using our data. Similarly, our data are only available for two plot sizes, hence do not cover a sufficient range of scales to allow for robust testing of their effects on the patterns of species richness and species diversity  $H'$  (Fridley et al. 2004, Herben et al. 2004).

#### *Beyond species identity: generalization across plant strategies*

Based on the magnitude of impact, our study species can be divided into three groups, in terms of their dispersal and competitive abilities. It is important to note that dominant taxa with the most profound negative impacts on species richness and diversity (*Calamagrostis epigejos*, *Phalaris arundinacea*, *Reynoutria xbohemica*, *Urtica dioica*) possess the most suitable strategy for successful spread – they are both capable of rapid colonization of new sites and persist in places colonized in the course of succession. The tufts with a hemicyptophytic arrangement of buds can block the space below-ground (by woody rhizomes) as well as on the surface by producing a thick layer of litter. All four taxa form long rhizomes, and their juveniles grow fast, rapidly pre-empting the available space. However, this needs to be accompanied by the ability to colonize and spread fast, which is especially important after major disturbances. *Calamagrostis epigejos* and *U. dioica* produce plenty of light wind-dispersed seeds, while *P. arundinacea* and *R. xbohemica* spread rapidly by proliferating fragments buried in the soil.

On the opposite side of the impact gradient, the native species *Cirsium arvense*, *C. heterophyllum*, *C. oleraceum* and *Tanacetum vulgare* represent weak dominants with minor impacts on community richness and diversity. They spread relatively slowly, are not strong competitors, and *C. arvense* often produces almost no seed as a result of intense herbivory in central Europe (Cripps et al. 2011). The success of these species is mediated by a continuous supply of disturbed sites, such as abandoned fields or meadows.

Other species studied have mostly an intermediate impact on community richness and diversity. *Petasites hybridus* and *Rumex alpinus* have thick but short rhizomes, which makes them rather slow colonizers. The annual *Impatiens glandulifera*, monocarpic perennial *Heracleum mantegazzianum* and polycarpic perennial *Lupinus polyphyllus* represent non-clonal dominants that need to rely on seed for their spread to new sites, and subsequent space pre-emption. *Lupinus polyphyllus* enriches the soil with nitrogen by bacterial symbiosis and other species (e.g. *H. mantegazzianum*, *Rumex alpinus*) by litter turnover. Further, *H. mantegazzianum* produces a high amount of seed and imposes a strong shading effect (e.g. Moravcová et al. 2005, Pergl et al. 2006, Perglová et al. 2006). On the contrary, *L. polyphyllus* often suffers from fungal infections (Garibaldi et al. 2009).

Root:shoot ratio, as an important plant characteristics, might potentially contribute to explaining the differences between the dominants with a high versus low impact on either species richness or diversity (see e.g. Kiaer et al. 2013). However, as such data are not available for many species included in our study, especially those of alien origin, it is not possible to rigorously test the relation between the dominant species' impacts and the root:shoot ratio.

Similarly, allelopathy may be an important mechanism enabling dominant species, especially of alien origin, to suppress community diversity. Among the dominants included in our study, the following are reported to have allelopathic effects on neighbouring plants: *Calamagrostis epigejos* (Pruchniewicz and Halarewicz 2019), *Cirsium arvense* (Kazinczi et al. 2001), *Cirsium oleraceum* (Barabasz-Krasny et al. 2017), *Heracleum mantegazzianum* (Jandová et al. 2015), *Impatiens glandulifera* (Bieberich et al. 2018), *Lupinus polyphyllus* (Lyytinen and Lindström 2019), *Phalaris arundinacea* (Tomes 2013), *Reynoutria* sp. div. (Moravcová et al. 2011), *Rumex alpinus* (Štastná et al. 2010), *Solidago canadensis* (Abhilasha et al. 2008), *Tanacetum vulgare* (Hodisan & Csep 2010) and *Urtica dioica* (Khatami et al. 2017). However, it is generally difficult to separate allelopathy from the shading effect of the dominant species' canopy, as reported for *Reynoutria* (Moravcová et al. 2011) and it is widely acknowledged that the results of pot-experiments aiming to test the allelopathic effects do not easily translate to the situation in the field (e.g. Parepa & Bossdorf 2016). Therefore, the explanatory power of this variable is rather elusive in our study system.

#### *Invasion and expansion: two sides of the same coin*

Nutrient-rich habitats in central Europe represent a source of successful invaders worldwide (Hejda et al. 2015) and this also holds for the native dominants included in our study. The three native dominants with the strongest impacts on species richness and diversity are recorded as naturalized in numerous regions of the world (at the level of countries, states, districts, or islands, as defined by the GloNAF database; van Kleunen et al. 2015, 2019, Pyšek et al. 2017) – *Urtica dioica* in 86, *Phalaris arundinacea* in 59 and *Calamagrostis epigejos* in 23 regions. In addition, many native dominants included in our study are noxious invaders outside Europe, e.g. *P. arundinacea* invades wetlands in North America (Galatowitsch et al. 1999) and *Cirsium arvense* and *Tanacetum vulgare* invade temperate grasslands worldwide (Guggisberg et al. 2012, Wolf et al. 2012).

Therefore, even some native species with weak impact in our study have successfully naturalized beyond their native range, such as *Tanacetum vulgare* and *Cirsium arvense*,

recorded in 114 and 106 GloNAF regions, respectively (van Kleunen et al. 2019). That some native dominants with weak impacts are even more widely distributed worldwide than those that suppress species richness and diversity to the greatest extent supports the notion that superior invasiveness does not automatically translate into strong impact (Ricciardi & Cohen 2007, Horáčková et al. 2014). Still, the success elsewhere of species that are dominants in central-European communities suggests that their ability to suppress other species through building high cover and exerting competitive effect can be assumed.

The theory predicts that the success of invasive species is due to two contrasting but non-exclusive views, i.e. (i) intrinsic factors that make them inherently good invaders; or (ii) becoming invasive as a result of extrinsic ecological and genetic influences such as release from natural enemies, hybridization or other novel ecological and evolutionary interactions (Colautti et al. 2014). We suggest that the former mechanism fits for the majority of the native dominants in our study, and their competitiveness is responsible for the unclear distinction between the impacts of native vs. invasive dominants. A proper test of the effect of origin, whether or not the impact of invasive aliens is greater than that of native species, would be to include only those native species in the comparison that have not successfully naturalized or invaded elsewhere (as in e.g. Kubešová et al. 2010, see van Kleunen et al. 2010 for theoretical framework). In central Europe, however, the strong native dominants are very likely to invade elsewhere in the world (Pyšek et al. 2009, Phillips et al. 2010).

Invasions by alien and expansions of native plants are two aspects of the same process in the central-European landscape, i.e. the spread of species resulting in the reduction of plant diversity. Both groups benefit from current changes in land-use, such as large-scale eutrophication, habitat homogenization, abandonment of traditional management (mowing, grazing), and large-scale disturbances of unprecedented magnitude, leading to massive fluctuations in the levels of available resources (Davis et al. 2000, Chytrý et al. 2008b, Fridley & Sax 2014).

Our results point to the importance of experimental field studies to address the impact of invasive species (Hejda et al. 2009, Kumschick et al. 2015), which provide thorough insights into the role of underlying factors, including that of habitat and its interaction with species life histories. Information obtained by such studies is different from results of large-scale macroecological studies that are routinely used to generalize the role of habitats in invasion ecology (e.g. Maskell et al. 2006, Chytrý et al. 2008a, b, Pyšek et al. 2015), but their potential to reveal the impact of invasive species is limited to correlative evidence. At the same time, the logistics of data collection in experimental studies and restricted species pool meeting the criteria for inclusion make it difficult to generalize about the effect of species' origin and account for a complex context-dependence of plant invasions (González-Moreno 2014, Pyšek et al. 2020a) because of necessarily limited numbers of species included in such studies.

### *Implications for conservation of biodiversity*

We provide robust evidence that both invasions of aliens and expansions of native species represent a serious problem for the conservation of biodiversity. The spread of species representing both groups leads to the homogenization of landscapes by forming large

areas occupied by species-poor stands with a strong dominance of a single or a few species, either invasive or native. Nevertheless, it is very likely that the specific history of the Eurasian flora, namely the long-term presence of intense human pressure (di Castri 1989), has led to the evolution of strong native dominants with affinity to vegetation in human-made or heavily affected habitats. In many areas without such a long history of human disturbance (e.g. Hawaii, New Zealand), there are very few native dominants, if any, that compare to the invasive aliens in terms of aggressive spread and strongly negative impacts on vegetation (Hejda 2013).

To conserve biodiversity, measures should be adopted to mitigate not only invasive species' impacts but also that of native dominants spreading in the current landscape; this would be best achieved by promoting traditional management and land-use or by using biological control (Těšitel et al. 2017). At least on a limited spatial scale, maintaining the traditional management should be accompanied by avoiding large-scale disturbances (Catford et al. 2012). The majority of dominant species, expanding natives and invasive aliens alike, are nitrophilous, recruiting from and colonizing disturbed and/or eutrophic habitats (Davis et al. 2000, Blumenthal 2006, Dostál et al. 2013, Hejda et al. 2015). Adopting management measures to reduce eutrophication processes would limit the spread of both invasive and native dominant species, and possibly be an efficient way of conserving the diversity of vegetation at the landscape level.

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## Acknowledgements

This research was done within the project 17-19025S (Czech Science Foundation). PPy, MH and MV were also supported by EXPRO grant no. 19-28807X (Czech Science Foundation) and long-term research development project RVO 67985939 (Czech Academy of Sciences). We thank Tony Dixon for editing the final version of the manuscript and Zuzana Sixtová for technical assistance.

## Souhrn

Invazní druhy rostlin často vytváří rozsáhlé dominantní porosty s velmi omezeným výběrem těch nejdolnějších původních druhů. Stejný efekt ale mohou mít i původní dominantní druhy, které se v současné krajině šíří. V této práci proto srovnáváme vliv 10 dominantních druhů, které jsou ve střední Evropě původní a 9 druhů, které jsou zde invazní. Pro každý jsme vybrali na území České republiky lokality (v počtu 5–16 pro jednotlivé druhy) s dostatečně velkými populacemi, aby bylo možné do nich umístit snímky s vysokou i nízkou pokryvností příslušné dominanty. Do vegetačních snímků o rozměrech  $4 \times 4$  m byl umístěn snímek o rozměrech  $1 \times 1$  m, aby bylo možné srovnat vliv dominance druhu na různých prostorových škálách. V každém snímku byly zaznamenány druhy cévnatých rostlin a jejich pokryvnost byla vizuálně odhadnuta na procentuální škále. Vztah mezi pokryvností dominanty, počtem druhů a diverzitou, vyjádřenou Shannonovým indexem  $H'$ , byl testován pomocí regresních modelů se smíšenými efekty (LMM). Rozdíly ve vlivu původních a invazních dominant byly testovány pomocí LMM analýzy kovariance. V plochách  $4 \times 4$  m celkem 17 dominant (9 původních a 8 invazních) významně snižovalo počty druhů, ale pouze 7 dominant (4 původní a 3 invazní) snižovalo druhovou diverzitu. *Reynoutria xbohemica*, *Calamagrostis epigejos* a *Phalaris arundinacea* měly nejsilnější negativní vliv na počty druhů, *Reynoutria xbohemica*, *Phalaris arundinacea* a *Urtica dioica* nejvíce snižovaly druhovou diverzitu, vyjádřenou Shannonovým indexem  $H'$ . Výsledky na škále  $1 \times 1$  m byly obdobné. Model se všemi druhy neodhalil významné rozdíly ve vlivu původních a invazních dominant. Pomocí ordinační analýzy (DCA) byly vymezeny dvojice původních a invazních dominant, které rostou v podobných společenstvech; tímto způsobem bylo vytvořeno 27 dvojic na velké škále a 24 na malé, protože dominanty se vyskytují ve více typech společenstev a bylo tedy možné je párovat s více než jedním druhem z opačné skupiny. V plochách  $4 \times 4$  m měly původní dominanty silnější negativní vliv na počty druhů než jejich invazní protějšek ve třech případech



(*Calamagrostis epigejos*, *Cirsium oleraceum* a *Phalaris arundinacea*) a invazní dominanty ve dvou případech (*Aster novi-belgii* agg. a *Rumex alpinus*). Pouze invazní dominanty (*Aster novi-belgii* agg. a *Rumex alpinus*) měly větší negativní vliv také na druhovou diverzitu, a to ve čtyřech párových srovnáních. Pro plochy 1 × 1 m byl nalezen jediný významný rozdíl v impaktu mezi původní a invazní dominantou. Je zřejmé, že jak invazní, tak původní dominanty mohou mít zásadní negativní vliv na diverzitu rostlinných společenstev. Při snahách o ochranu vzácných druhů a společenstev je proto potřeba se zaměřit na minimalizaci vlivu dominantních druhů z obou skupin. Toho lze v mnoha případech dosáhnout podporou tradičního způsobu využívání krajiny, založeného na kombinaci kosení a pastvy.

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Received 22 March 2021

Revision received 15 June 2021

Accepted 16 June 2021