



Diversity loss in grasslands due to the increasing dominance of alien and native competitive herbs

Marta Czarniecka-Wiera¹ · Zygmunt Kącki¹ · Milan Chytrý² · Salza Palpurina^{2,3}

Received: 11 December 2017 / Revised: 11 April 2019 / Accepted: 6 June 2019 / Published online: 17 June 2019
© The Author(s) 2019

Abstract

The increasing dominance of competitive plant species may reduce species richness of plant communities. Yet, species richness may depend on spatial scale and the alien versus native status of the dominant species. To explore the dominance effects of alien versus native species on species richness, we sampled semi-natural grasslands in southwestern Poland. We established 100 m² squares at different grassland sites, and in two opposite corners we placed two series of five nested plots (0.001, 0.01, 0.1, 1 and 10 m²), in which we recorded all vascular plant species. Next, we selected squares with a strongly dominant plant in one corner (high-dominance series) and with no strong dominant in the opposite corner (low-dominance series). The number of species per plot and the slopes of the species–area curves fitted to each nested-plot series were used to assess whether the alien vs. native status of the dominant species influences species–richness pattern across scales. We found a significantly lower number of species in the high-dominance series than in the low-dominance series, regardless of the alien versus native status of the dominant species. The slopes of the species–area curves indicated that the rate of species accumulation with increasing area was faster in the high-dominance series than in the low-dominance series; however, this pattern did not depend on the alien vs. native status of the dominants. Our study confirms that increasing dominance is linked to a decline in species richness, but reveals that alien dominants do not have a stronger impact than native dominants.

Keywords Competitive exclusion · Dominance · Plant invasions · Species–area relationship · Species richness · Temperate grasslands

Communicated by Daniel Sanchez Mata.

This article belongs to the Topical Collection: Invasive species.

✉ Marta Czarniecka-Wiera
m.czarniecka86@gmail.com

¹ Department of Vegetation Ecology, Botanical Garden, University of Wrocław, S. Przybyszewskiego 63, 51-148 Wrocław, Poland

² Department of Botany and Zoology, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic

³ Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Acad. G. Bonchev bl. 23, 1113 Sofia, Bulgaria

Introduction

Semi-natural grasslands are important habitats for biodiversity conservation in European agricultural landscapes (Duelli and Obrist 2003; Tscharnke et al. 2005; Bonari et al. 2017). For centuries, these habitats have been used primarily for animal husbandry; however, this function has recently become less important due to decreasing livestock production (MacDonald et al. 2000; Poschlod et al. 2005; Wehn et al. 2017). As a consequence, many semi-natural grasslands have been abandoned, afforested or converted into arable land or intensively managed grasslands (Falcucci et al. 2007; Prévosto et al. 2011). Changes in land use and in the management of semi-natural grasslands have led to the encroachment of trees and shrubs and to the expansion of alien or native competitors, which tend to dominate ecosystems (Hansson and Fogelfors 2000; Young et al. 2005).

Several studies have suggested that alien species invasions cause a decline in species richness (henceforth SR) of native plant communities (Parker et al. 1999; Byers et al. 2002; Hejda et al. 2009). This phenomenon is linked to the ability of alien species to become dominant in a plant community outside its native range and to locally replace native species (Pyšek and Pyšek 1995; Hejda and Pyšek 2006; Chmura et al. 2015). The evolution of increased competitive ability (EICA hypothesis; Callaway and Ridenour 2004) suggests that once separated from their natural enemies, alien species evolve to use more resources to develop competitive traits, e.g. larger size and increased fecundity. However, the relative abundance of native species can also increase in the changing environment. For example, after cessation of mowing and grazing in grasslands, species which represented a low proportion of the biomass of the managed grasslands can expand and attain dominance, resulting in a decrease in community SR (Falińska 1991). Examples of native European grassland plants that are becoming dominant with negative effects on SR include *Brachypodium pinnatum* in semi-dry grasslands (Bobbink et al. 1987), *Molinia caerulea* in wet meadows (Lepš 2004), *Calamagrostis villosa* in acidic sub-alpine grasslands (Hejman et al. 2009) and *Calamagrostis epigejos* or *Stipa pulcherrima* in steppe grasslands (Házi et al. 2011; Ruprecht et al. 2016). It is not fully understood whether dominant alien plant species have a stronger impact on SR than dominant native plant species.

The effect of dominant species on SR depends on the sampling scale because species interactions tend to be intense within small areas, but weakening in larger areas where environmental heterogeneity tends to separate different species in space, thus reducing direct contact between plant individuals (Tilman and Pacala 1993). This scale-dependent effect is observable in studies on the impact of alien species' dominance on biodiversity: fine-scale studies more often suggest that invasive species are a threat to biodiversity (Gerber et al. 2008; Vilà et al. 2011), whereas coarse-scale studies tend to report a negligible impact (Planty-Tabacchi et al. 1996; Maskell et al. 2006). Powell et al. (2013) related this scale-dependent effect of invasive species on SR to the species–area relationship (SAR). They sampled paired forest plots with and without invasive species and found that the decline in the number of species at the invaded sites, compared with that at non-invaded sites, was larger in smaller plots than in larger plots. However, many studies have highlighted that the SAR depends on the plant community type (Crawley and Harral 2001; Drakare et al. 2006; Dolnik and Breuer 2008). It is, therefore, unclear whether the pattern observed by Powell et al. (2013) is valid in other community types, such as grasslands.

In the present study, we compare the effects of dominant species, either alien or native, on SR of semi-natural grasslands to answer the following questions: (1) Does a decline in SR depend on the presence of a single strong dominant species in the plant community? If

so, does this decline depend on (2) spatial scale and (3) the alien versus native origin of the dominant plant species?

Materials and methods

Study area

The study area is located in the Sudetes Mountains in southwestern Poland ($50^{\circ}0'–50^{\circ}10'N$, $15^{\circ}20'–16^{\circ}55'E$, 3800 km^2 , $290–841\text{ m a.s.l.}$; Fig. 1). The mean annual temperature ranges from 5 to $8\text{ }^{\circ}\text{C}$ and the annual precipitation from 490 to 650 mm (Woś 1999). The bedrock consists of acidic and poorly weathered magmatic and metamorphic rocks (Walczak 1968). The vegetation studied includes semi-natural meadows belonging mainly to the phytosociological alliances *Arrhenatherion* and *Polygono-Trisetion* (Kącki et al. 2013). Since the 1980s, large areas of meadows in the Sudetes have been abandoned and subsequently overgrown by competitive herbaceous plant species, including some aliens (Biała and Żyszkowska 2004).

Sampling design

We sampled grasslands across the Sudetes from 2012 to 2014. The sampling sites were selected randomly within grassland areas using digital maps provided by the Institute of Technology and Life Sciences in Falenty, Poland. The maps included Digital Terrain Model (with elevation, slope and aspect), land cover and soil types (Nadolna and Żyszkowska 2011). Using ArcGIS 9.3, we overlaid the Sudetes with a $10\times 10\text{-km}$ grid and selected grid cells with $>25\%$ grassland cover. In each selected grid cell, we placed five random points in grassland areas and created a circular buffer zone of 250 m radius

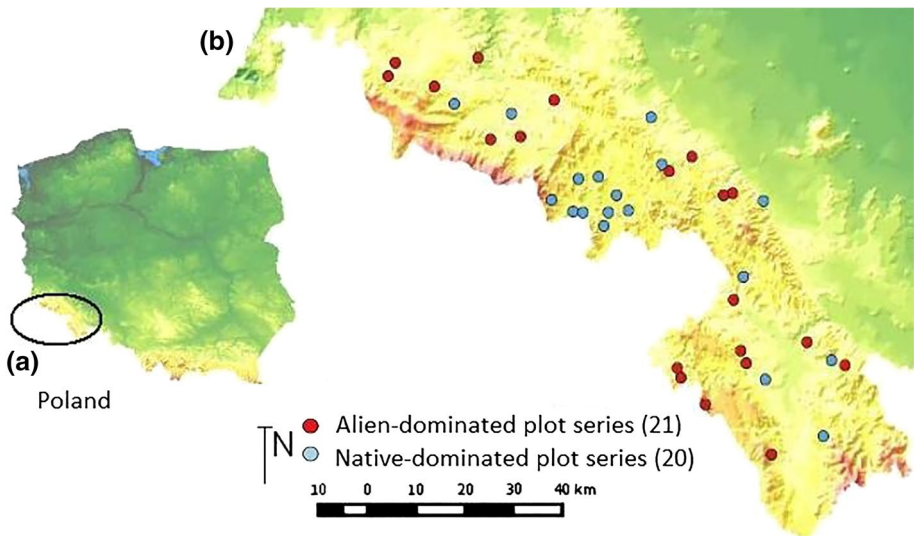


Fig. 1 Location of the 41 sampled paired nested-plot series in the Polish part of the Sudetes Mountains (<http://www.codgik.gov.pl/index.php/darmowe-dane/nmt-100.html>. Accessed 2nd Oct 2018)

around each point. To avoid overlaps between the buffer zones, we ensured that the minimum distance between random points was 1 km. During the field survey, within each buffer zone, we selected a single vegetation stand with an alien plant species that was as close as possible to the central point of its buffer zone. If no alien species were found within the buffer zone, a vegetation stand without alien species at the central point was selected. In each vegetation stand, we established a square of 100 m² at a place that was as homogeneous as possible in terms of topography and vegetation physiognomy. Next, in two opposite corners of the 100 m² square, we placed a series of five squared nested plots of increasing sizes (in m²) as follows: 0.001, 0.01, 0.1, 1 and 10 (Fig. 2; Dengler 2009). In each nested-plot series, the presence of shoots of all species of vascular plants was recorded. The percentage cover of each species was visually estimated in the largest nested plot (10 m²) of the series. The vegetation data are stored in the *Polish Vegetation Database* (Kački and Śliwiński 2012).

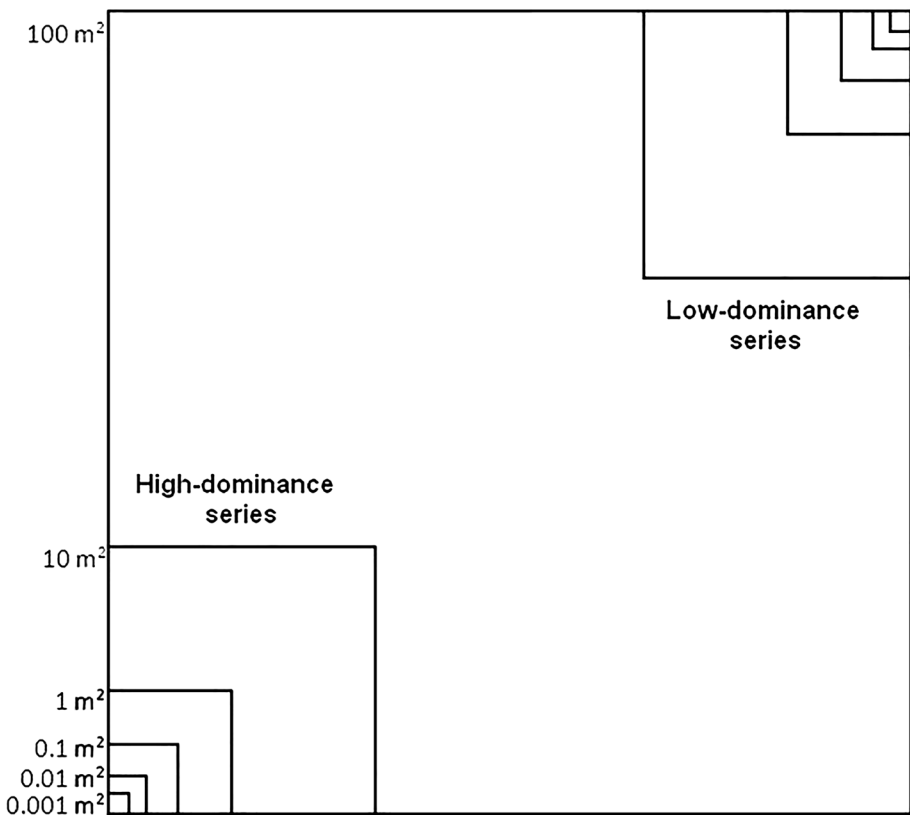


Fig. 2 Plot sampling design. Paired series of nested plots measuring between 0.001 and 10 m² were arranged in two opposite corners of each 100 m² square. The high-dominance (HD) series include plots in which the cover of the most abundant species was at least 20% higher than the cover of the most abundant species in the other (low-dominance, LD) series. Note that the plot size is not on a true scale

Dataset and statistical analyses

We collected data from 198 squares of 100 m², each with two nested-plot series located in two opposite corners of the square. For analyses, we selected a subset of those squares in which the cover of the most abundant species in the largest plot of the nested-plot series (10 m²) in one corner (high-dominance series, henceforth HD series) was at least 20% higher than the cover of the most abundant species in the largest plot of the series in the opposite corner (low-dominance series, henceforth LD series). However, to acknowledge the possible effects of varying threshold differences in cover, we tested their effects on SR and the rate of species accumulation with increasing area. We used eight thresholds from 10 to 70% (as we did not have plots with a larger difference in cover above 70%) with 10 unit increments.

Application of this criterion resulted in the selection of 62 squares. These squares were further divided into the following subsets: (1) alien-dominated subset, in which the dominant species in the HD series was alien and there were no aliens in the LD series (n = 21); (2) native-dominated subset, in which the dominant species in the HD series was native, and there were no aliens in the LD series (n = 20); (3) the dominant species in the HD series was native, but there were also aliens (not dominant) in the LD series (n = 21). We excluded the third subset from the analysis to avoid any influence of alien species in the LD series on SR. In our final selection of 41 squares (Fig. 1), the dominant alien species were *Solidago gigantea*, *S. canadensis*, *Lupinus polyphyllus* and *Reynoutria sachalinensis*, whereas the dominant native species were *Carex brizoides*, *Agrostis capillaris*, *Festuca rubra*, *Galium mollugo* s. l., *Lathyrus pratensis* and *Calamagrostis epigejos* (Table 1). The species names are given following the Euro + Med PlantBase (<http://www.emplantbase.org/home.html>, Accessed 2nd Nov 2018).

As a measure of SR, we used the number of all vascular plant species per single nested plot. The dependence between dominance and SR was assessed by comparing SR between the HD and LD series using paired Student's *t* test (after Bonferroni correction). The analyses were applied separately for each plot size across all pairs of nested-plot series regardless of the status of the dominant species (n = 5 × 41) and separately for the alien-dominated and native-dominated subsets.

To assess the magnitude of the effect of dominant species on SR, we calculated standardised difference in SR between the high-dominance and low-dominance series (δ_{SR} , %) as follows: $\delta_{SR} = \frac{(SR_{HD} - SR_{LD})}{SR_{LD}} \times 100$, where SR is species richness, HD is the high-dominance series of nested plots and LD is the low-dominance series of nested plots. $\delta_{SR} = 0\%$ means that there is no difference in terms of SR between the HD and LD series and $\delta_{SR} = -50\%$ means that the SR in the HD series is half of that in the LD series. We then used ANOVA (after Bonferroni correction) to test whether the mean δ_{SR} differed between the alien-dominated and native-dominated subsets.

We used SAR to measure the rate of species accumulation with increasing area. SAR can be modelled using the power-law function $S = cA^z$, where *S* is the number of species and *A* is the sampling area. The model parameters *c* and *z* express the expected mean SR per unit area and the rate of species accumulation with an increase in sampling area, respectively (Arrhenius 1921; Rosenzweig 1995; Dolnik and Breuer 2008). We used the *power* function in the 'mmSAR' package (Guilhaumon et al. 2010) to fit the power-law function to each nested-plot series. We then used paired *t*-tests to check whether the obtained *c*- and *z*-values differed significantly between the paired HD and LD series across both subsets.

Table 1 Summary of plant species richness across the dataset

	n	Cover range in high-dominance series (%)	Species richness in low-dominance series (mean ± SD)	Species richness in high-dominance series (mean ± SD)	z-value in low-dominance series (mean ± SD)	z-value in high-dominance series (mean ± SD)	c-value in low-dominance series (mean ± SD)	c-value in high-dominance series (mean ± SD)
All plots	41	45–100	22.9 ± 7.4	15.4 ± 7.0	0.16 ± 0.04	0.20 ± 0.06	15.3 ± 5.2	9.6 ± 4.6
Set of plots with alien dominant species	21	45–100	20.2 ± 5.9	14.2 ± 6.5	0.16 ± 0.05	0.19 ± 0.07	13.6 ± 4.2	9.0 ± 4.4
<i>Solidago gigantea</i>	7	60–98	20.4 ± 3.2	13.1 ± 5.9	0.18 ± 0.04	0.23 ± 0.10	12.9 ± 1.9	7.9 ± 4.0
<i>Solidago canadensis</i>	10	50–100	17.4 ± 5.9	12.0 ± 5.8	0.16 ± 0.05	0.20 ± 0.04	11.5 ± 3.4	7.5 ± 3.7
<i>Lupinus polyphyllus</i>	3	45–60	27.0 ± 5.2	24.0 ± 1.7	0.16 ± 0.04	0.18 ± 0.02	19.8 ± 5.0	15.7 ± 1.8
<i>Reynoutria sachalinensis</i>	1	85	26	14	0.14	0.20	18.7	8.3
Set of plots with native dominant species	20	45–100	25.9 ± 7.9	17.3 ± 7.5	0.16 ± 0.03	0.20 ± 0.06	17.5 ± 5.2	10.9 ± 5.0
<i>Carex brizoides</i>	11	70–100	25.9 ± 8.0	12.9 ± 5.2	0.16 ± 0.04	0.22 ± 0.06	17.4 ± 5.4	7.6 ± 2.8
<i>Agrostis capillaris</i>	4	50–80	24.5 ± 5.7	22.0 ± 5.6	0.17 ± 0.02	0.19 ± 0.05	16.1 ± 4.0	14.3 ± 3.9
<i>Festuca rubra</i>	2	60	32.5 ± 7.5	31.0 ± 2.0	0.16 ± 0.04	0.17 ± 0.02	22.1 ± 2.7	20.6 ± 0.2
<i>Galium mollugo</i> s.l.	1	45	15	14	0.14	0.15	12.1	9.3
<i>Lathyrus pratensis</i>	1	65	24	18	0.11	0.13	17.3	13.8
<i>Calamagrostis epigejos</i>	1	80	33	21	0.15	0.31	22.4	10.1

* number of paired nested-plot series

To test whether the magnitude of the dominance effect depends on the alien vs. native status of the dominant species, we calculated the difference in c - and z -values between HD and LD series (i.e. $\delta_c = c_{HD} - c_{LD}$, $\delta_z = z_{HD} - z_{LD}$) and tested by means of ANOVA whether δ_c and δ_z differed between the alien- and the native-dominated subset.

Results

Paired t -test revealed that SR was significantly lower in the HD series than in the LD series (Fig. 3). This was valid for the entire dataset (Fig. 3a) and for the alien- or native-dominated subsets (Fig. 3b, c). The mean standardized difference in SR (δ_{SR}) did not differ between the alien-dominated and native-dominated subsets (Fig. 4).

Paired t -tests revealed that c -values were significantly lower in the HD series than in the LD series, whereas z -values were significantly higher in the HD series than in the LD series. This means that the mean SR per unit area was lower for the HD series, but its increase with plot size was faster than in the LD series (Fig. 5). However, ANOVA tests for c - and z -values showed no significant difference between the alien- and native-dominated subsets (Fig. 6).

Individual dominant plant species were found to have influenced SR and SAR parameters. The largest difference between the HD and LD series for SR as well as c - and z -values of SAR were found for *Solidago gigantea* (alien), *S. canadensis* (alien) and *Carex brizoides* (native) and the lowest for *Lupinus polyphyllus* (alien) and *Agrostis capillaris* (native) (Table 1).

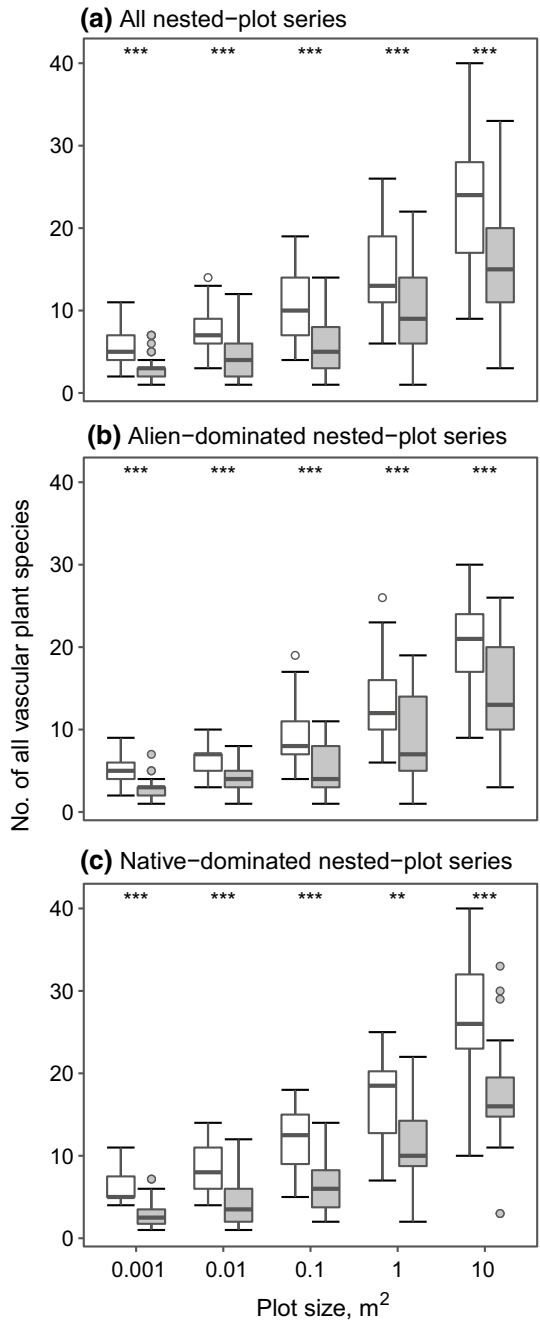
We found that larger threshold difference in cover for considering a species to be dominant corresponds to larger difference in SR as well as in c - and z -values between the HD and LD series (“Appendix 1”). In other words, the larger the difference in cover between the most abundant species in one series and the most abundant species in the other series in a pair, the stronger is its effect on SR and species-accumulation rate.

Discussion

Dominance is one of the main factors that affect species coexistence in plant communities (Whittaker 1965; Hillebrand et al. 2008). In the present study, we asked whether the decline in SR depends on the presence of a strong dominant species in the plant community. We provided evidence that grassland plant communities with strongly dominant herbaceous species tend to be more species-poor than communities with less dominant species. The observed significant difference in SR can be explained by interspecific competitive interactions which lead to the dominance of a few or just one species in the community (Tilman and Pacala 1993). A decline in SR with increasing dominance was observed in many ecosystems, such as forests (de la Cretaz and Kelty 1999), open water (Zehnsdorf et al. 2015), and dry grasslands (Dostálek and Frantík 2012), suggesting that it is a common phenomenon.

We also asked whether the magnitude of the decline in SR depends on the spatial scale. We found that the dominance of competitive plants changed the SR pattern in the studied grasslands. We also found that the rate of species accumulation with increasing plot size (as estimated by the z -value of the SAR) was higher in the high dominance grasslands than in the low dominance grasslands, suggesting a stronger negative

Fig. 3 Species richness (the number of vascular plant species per plot; SR) compared between the high-dominance (HD, grey) and low-dominance (LD, white) series of all paired nested plots, $n = 41$ (a), for the alien-dominated subset, $n = 21$ (b), and for the native-dominated subset, $n = 20$ (c). The boxes represent interquartile ranges, the horizontal lines within boxes represent medians, the whiskers represent outliers, and the white and grey points represent extreme values. Differences in SR between the HD and LD series were tested separately for each plot size using Student's t -test for paired samples (after Bonferroni correction): * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$



effect of dominance on SR in small areas. In small areas, the competition among species is stronger, leading to the extinction of less competitive species, whereas on a broader scale, the impact of the dominant competitors is less pronounced because there are more

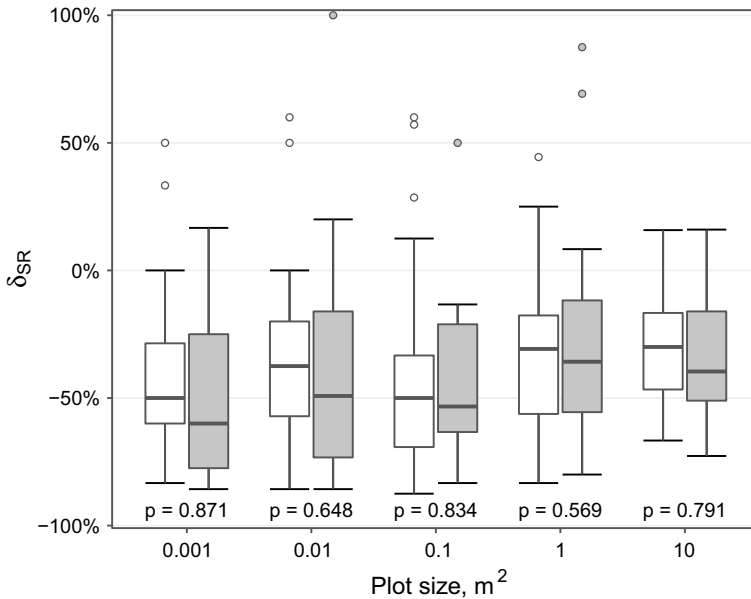


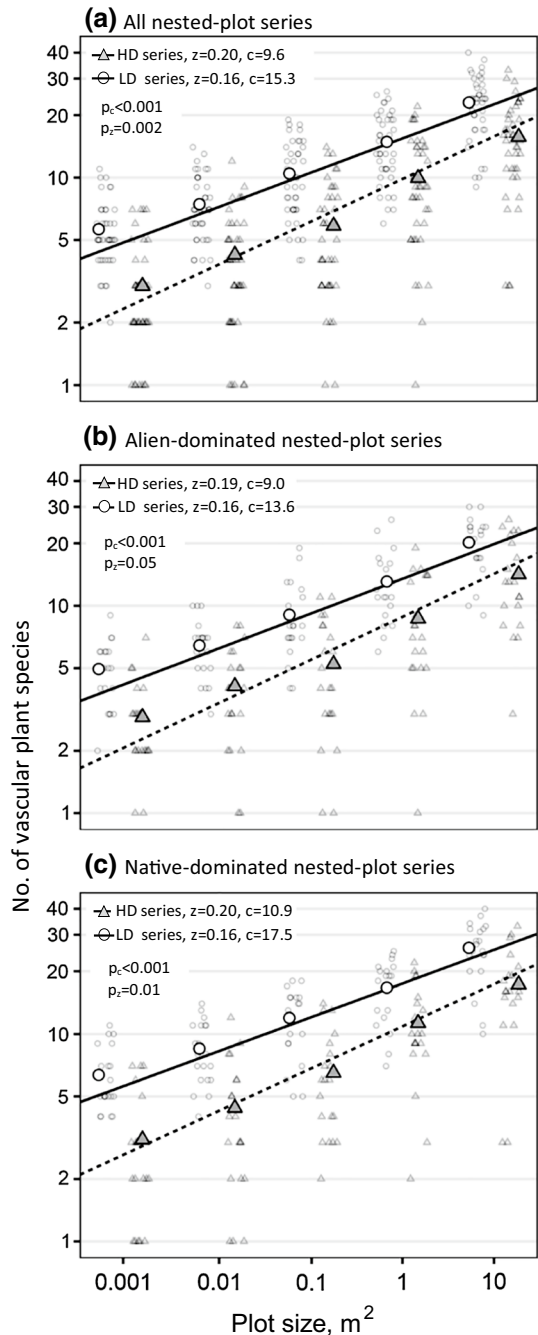
Fig. 4 Standardized difference in species richness between the high-dominance (HD) and low-dominance (LD) series of nested plots (δ_{SR} , %) illustrated for alien-dominated (white) and native-dominated (grey) subsets of series. Statistical significance between alien- and native-dominated subsets of series was tested by means of ANOVA (after Bonferroni correction)

opportunities for species with similar ecological requirements to avoid competition by growing in different places (Godsoe et al. 2015).

Finally, we found no evidence that the effect of dominance on SR and the species accumulation rate would be stronger for alien species than for native ones. This dominance effect is well known for alien species (Gerber et al. 2008; Vilà et al. 2011), but it has been less studied for native species (Hansson and Fogelfors 2000; Csergő et al. 2013). Our results are similar to those presented by Meiners et al. (2001) in their long-term observational study of abandoned agricultural fields. They found that the increasing dominance of alien and native plants during old-field succession had a similar effect on SR. Opposite conclusions were presented by Vilà and Weiner (2004), who reviewed the published data and found that alien dominant plants have a stronger impact on the community structure than native dominant plants. However, they noted that most studies focus on species that are well known for their high invasiveness and negative effects on the diversity of invaded plant communities.

In the present study, the most important dominant species which influenced SR and the rate of species accumulation with increasing area were found among both alien (*Solidago gigantea* and *S. canadensis*) and native species (*Carex brizoides*). It is likely that the tall height or high biomass production of these plants is responsible for their strong negative effect on biodiversity, especially through increasing competition for light (Jakobs et al. 2004; Chmura and Sierka 2007; Divišek et al. 2018). Experimental studies also confirm that one of the most important traits of competitors is a high growth rate and high biomass production (Gaudet and Keddy 1988; Szymura and Szymura 2015). Other dominant species such as *Lupinus polyphyllus* (alien) and *Agrostis capillaris* (native) had minor impacts

Fig. 5 Comparisons of the log–log species–area curves between the high-dominance (HD) and low-dominance (LD) series of nested plots. The power-law function was fitted to the mean species richness for each plot size across all series. The big black symbols represent mean species richness per unit area (c -value), while the small grey symbols represent single values of species richness. The slopes of the lines are interpreted as the rate of species accumulation with increasing sampling area (z -value). The differences in c - and z -values between the HD and LD series within each 100-m² square were tested using Student's t -test for paired samples. Note that single points were jittered along the x -axis to avoid overlapping



on SR and the rate of species accumulation with increasing area. The negligible effect of *L. polyphyllus* can be explained by its patchy growth, which allows other species to occupy empty patches (Hejda 2013), while *A. capillaris* is a medium-tall grass with narrow leaves and relatively sparse stands with limited shading effect. Further, *A. capillaris* is native to

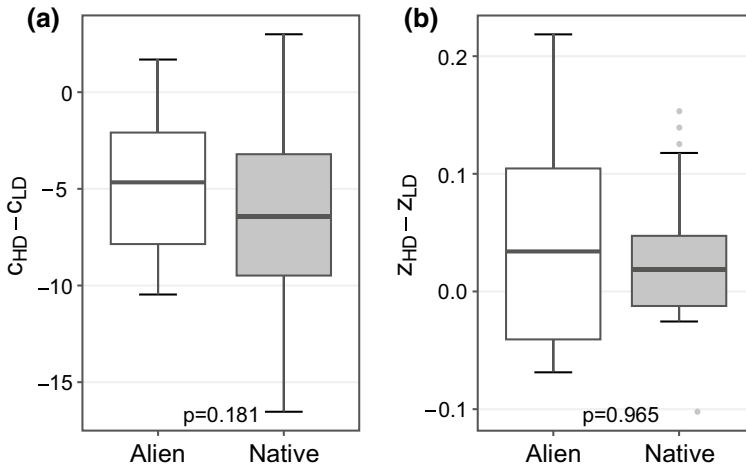


Fig. 6 A comparison of differences in the effect of species dominance on the species-area relationship between the alien-dominated and the native-dominated subsets. The effect of species dominance ($c = c_{HD} - c_{LD}$; $z = z_{HD} - z_{LD}$) is measured as the difference in c -value (a) and z -value (b) of the species-area relationship between the high-dominance (HD) and low-dominance (LD) series of nested plots within each alien-dominated or native-dominated subset. Statistical significance was tested by means of ANOVA

Europe but alien to Asia, Australia and North America, where it is known as a strong competitor that causes a decrease in the cover of native species (Johnston and Pickering 2001).

Although our results suggest that alien and native species have similar impacts on SR and on the rate of species accumulation with increasing area, we should note that, in general, different factors are related to the dominance of alien or native plant species. Studies on plant invasions have shown that dominance of alien species is positively correlated with several factors including landscape fragmentation (Vilà and Ibáñez 2011), disturbances (Deuschewitz et al. 2003) and propagule pressure (Lonsdale 1999), whereas increasing dominance of native plant species is often connected with changes in agricultural management (Bobbink et al. 1987; Hejerman et al. 2009). However, comparative studies of factors affecting the dominance of alien versus native species are scarce. Seabloom et al. (2015) found that the cover of alien species increased more than the cover of native species after nutrient additions, while higher native species cover was strongly connected with the cessation of grazing. More comparative studies are needed to obtain a better understanding of the phenomenon of increasing dominance of alien versus native species.

The observed negative impact of strong native competitors on biodiversity (Bobbink et al. 1987; de la Cretaz and Kelty 1999; Ervin and Wetzel 2002; Chmura and Sierka 2007; Daleo et al. 2017) has motivated a discussion on how species are classified as invasive. Some experts have proposed that problematic native species can also be classified as invasive (Alpert et al. 2000; Valery et al. 2008). Our results are consistent with this point of view, showing that native plant species capable of becoming dominant are threatening local biodiversity to a similar degree as alien species. To avoid terminological confusion, we favour the use of the term ‘expansive species’, which has been proposed for native species that increase in abundance following environmental changes (Richardson et al. 2000; Pyšek et al. 2004).

The decrease in SR resulting from the increased dominance of a competitively strong species is a major concern from the perspective of nature conservation. Our results suggest

that both alien and native dominant plants can threaten fine-scale plant diversity in temperate grasslands. Plant species which are superior competitors can significantly reduce SR in grasslands regardless of whether they are alien or native. A task for nature conservation is to categorise expanding dominant plants not only based on their origin but particularly based on the severity of their species-specific effects on biodiversity. Such categorization would be more important for prioritising management efforts than the simple dichotomy between alien and native species.

Acknowledgements The work of MC and SP was supported by the Czech Science Foundation (project 14-36079G, Centre of Excellence PLADIAS).

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

Appendix 1

See Table 2.

Table 2 The changes in species richness and SAR parameters according to different thresholds of dominance

Difference in the cover between the dominant species in HD series and the most abundant species in the LD series (%) ^a	Number of the paired nested-plots series	Cover range in the HD series (%)	Cover range in the LD series (%)	Species richness in the LD series (mean)	Species richness in the HD series (mean)	Difference in species richness between the LD and HD series (mean)	z-value in the LD series (mean)	z-value in the HD series (mean)	Difference in z-values between the HD and LD series (mean)	c-value in the LD series (mean)	c-value in the HD series (mean)	Difference in c-values between the LD and HD series (mean)
10	65	30–100	15–60	24	19	5	0.168	0.188	0.021	16.31	12.32	3.99
20	41	45–100	15–60	22	15	7	0.164	0.193	0.029	15.48	9.85	5.63
30	31	45–100	15–60	22	14	8	0.160	0.205	0.045	15.28	8.47	6.81
40	28	60–100	15–60	21	13	8	0.162	0.207	0.046	14.41	7.90	6.51
50	20	80–100	15–40	23	12	11	0.158	0.213	0.055	15.46	7.36	8.10
60	14	80–100	15–30	21	12	10	0.157	0.214	0.057	14.36	7.12	7.24
70	8	85–100	15–30	18	10	8	0.140	0.192	0.052	12.39	6.15	6.24
80	No data	No data	No data	No data	No data	No data	No data	No data	No data	No data	No data	No data

^aThe cover of the dominant species in the HD series and the most abundant species in the LD series was estimated for the largest (10 m²) plot of the series

References

- Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *PPEES* 3:52–66. <https://doi.org/10.1078/1433-8319-00004>
- Arrhenius O (1921) Species and area. *J Ecol* 9:95–99. <https://doi.org/10.2307/2255763>
- Biała K, Żyszkowska M (2004) Effects of changes in grassland management on biodiversity and landscape in the Sudeten Mountains in Poland. *Grassl Sci Eur* 4:210–212
- Bobbink R, During HJ, Schreurs J, Willems J, Zielman R (1987) Effects of selective clipping and mowing time on species diversity in chalk grassland. *Folia Geobot Phytotax* 22:363–376. <https://doi.org/10.1007/BF02853233>
- Bonari G, Fajmon K, Malenovský I, Zelený D, Holuša J, Jongepierová I, Kočárek P, Uříčář J, Chytrý M (2017) Management of semi-natural grasslands benefiting both plant and insect diversity: the importance of heterogeneity and tradition. *Agric Ecosyst Environ* 246:243–252. <https://doi.org/10.1016/j.agee.2017.06.010>
- Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky E, Hayes D (2002) Directing research to reduce the impacts of nonindigenous species. *Conserv Biol* 16:630–640. <https://doi.org/10.1046/j.1523-1739.2002.01057.x>
- Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Front Ecol Environ* 2:436–443. [https://doi.org/10.1890/1540-9295\(2004\)002%5B0436:NWISAT%5D2.0.CO;2](https://doi.org/10.1890/1540-9295(2004)002%5B0436:NWISAT%5D2.0.CO;2)
- Chmura D, Sierka E (2007) The invisibility of deciduous forest communities after disturbance: a case study of *Carex brizoides* and *Impatiens parviflora* invasion. *For Ecol Manage* 242:487–495. <https://doi.org/10.1016/j.foreco.2007.01.083>
- Chmura D, Tokarska-Guzik B, Nowak T, Woźniak G, Bzdęga K, Koszela K, Gancarek M (2015) The influence of invasive *Fallopia* taxa on resident plant species in two river valleys (southern Poland). *Acta Soc Bot Pol* 84:23–33. <https://doi.org/10.5586/asbp.2015.008>
- Crawley MJ, Harral JE (2001) Scale dependence in plant biodiversity. *Science* 291:864–868. <https://doi.org/10.1126/science.291.5505.864>
- Csergő AM, Demeter L, Turkington R (2013) Declining diversity in abandoned grasslands of the Carpathian Mountains: do dominant species matter? *PLoS ONE* 8:e73533. <https://doi.org/10.1371/journal.pone.0073533>
- Daleo P, Alberti J, Bruschetti CM, Martinetto P, Pascual J, Iribarne O (2017) Herbivory and presence of a dominant competitor interactively affect salt marsh plant diversity. *J Veg Sci* 28:1178–1186. <https://doi.org/10.1111/jvs.12574>
- de la Cretaz AL, Kelty MJ (1999) Establishment and control of hay-scented fern: a native invasive species. *Biol Invasions* 1:223–236. <https://doi.org/10.1023/A:1010098316832>
- Dengler J (2009) A flexible multi-scale approach for standardized recording of plant species richness patterns. *Ecol Indic* 9:1169–1178. <https://doi.org/10.1016/j.ecolind.2009.02.002>
- Deutschewitz K, Lausch A, Kühn I, Klotz S (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecol Biogeogr* 12:299–311. <https://doi.org/10.1046/j.1466-822X.2003.00025.x>
- Divíšek J, Chytrý M, Beckage B, Gotelli NJ, Lososová Z, Pyšek P, Molofsky J (2018) Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. *Nat Commun* 9:art.4631. <https://doi.org/10.1038/s41467-018-06995-4>
- Dolnik C, Breuer M (2008) Scale dependency in the species–area relationship of plant communities. *Folia Geobot* 43:305–318. <https://doi.org/10.1007/s12224-008-9019-4>
- Dostálek J, Frantík T (2012) The impact of different grazing periods in dry grasslands on the expansive grass *Arrhenatherum elatius* L. and on woody species. *Environ Manage* 49:855–861. <https://doi.org/10.1007/s00267-012-9819-4>
- Drakare S, Lennon JJ, Hillebrand H (2006) The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecol Lett* 9:215–227. <https://doi.org/10.1111/j.1461-0248.2005.00848.x>
- Duelll P, Obrist MK (2003) Regional biodiversity in an agricultural landscape: the contribution of semi-natural habitat islands. *Basic Appl Ecol* 4:129–138. <https://doi.org/10.1078/1439-1791-00140>
- Ervin GN, Wetzel RG (2002) Influence of a dominant macrophyte, *Juncus effusus*, on wetland plant species richness, diversity, and community composition. *Oecologia* 130:626–636. <https://doi.org/10.1007/s00442-001-0844-x>
- Euro + Med (2006–2018): Euro + Med PlantBase—the information resource for Euro-Mediterranean plant diversity. <http://ww2.bgbm.org/EuroPlusMed/>. Accessed 2 Nov 2018

- Falcucci A, Maiorano L, Boitani L (2007) Changes in landuse/land-cover patterns in Italy and their implications for biodiversity conservation. *Landsc Ecol* 22:617–631. <https://doi.org/10.1007/s10980-006-9056-4>
- Falińska K (1991) Plant demography in vegetation succession. *Tasks Veg Sci* 26:1–210
- Gaudet CL, Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. *Nature* 334:242–243. <https://doi.org/10.1038/334242a0>
- Gerber E, Krebs C, Murrell C, Moretti M, Rocklin R, Schaffner U (2008) Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biol Conserv* 141:646–654. <https://doi.org/10.1016/j.biocon.2007.12.009>
- Godsoe W, Murray R, Plank MJ (2015) The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography* 38:1071–1079. <https://doi.org/10.1111/ecog.01134>
- Guilhaumon F, Mouillot D, Gimenez O (2010) mmSAR: an R-package for multimodel species–area relationship inference. *Ecography* 33:420–424. <https://doi.org/10.1111/j.1600-0587.2010.06304.x>
- Hansson M, Fogelfors H (2000) Management of a semi-natural grassland; results from a 15-year-old experiment in southern Sweden. *J Veg Sci* 11:31–38. <https://doi.org/10.2307/3236772>
- Házi J, Bartha S, Szentés S, Wichmann B, Penksza K (2011) SeminatURAL grassland management by mowing of *Calamagrostis epigejos* in Hungary. *Plant Biosyst* 145:699–707. <https://doi.org/10.1080/11263504.2011.601339>
- Hejzman M, Česková M, Hejzmanová P, Pavlí V, Jones M (2009) Expansion of *Calamagrostis villosa* in sub-alpine *Nardus stricta* grassland: Cessation of cutting management or high nitrogen deposition? *Agric Ecosyst Environ* 129:91–96. <https://doi.org/10.1016/j.agee.2008.07.007>
- Hejda M (2013) Do species differ in their ability to coexist with the dominant alien *Lupinus polyphyllus*? A comparison between two distinct invaded ranges and a native range. *NeoBiota* 17:39–55. <https://doi.org/10.3897/neobiota.17.4317>
- Hejda M, Pyšek P (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biol Conserv* 132:143–152. <https://doi.org/10.1016/j.biocon.2006.03.025>
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J Ecol* 97:393–403. <https://doi.org/10.1111/j.1365-2745.2009.01480.x>
- Hillebrand H, Bennett DM, Cadotte MW (2008) Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89:1510–1520. <https://doi.org/10.1890/07-1053.1>
- Jakobs G, Weber E, Edwards PJ (2004) Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Divers Distrib* 10:11–19. <https://doi.org/10.1111/j.1472-4642.2004.00052.x>
- Johnston FM, Pickering CM (2001) Alien plants in the Australian Alps. *Mt Res Dev* 21:284–291. [https://doi.org/10.1659/0276-4741\(2001\)021%5B0284:APITAA%5D2.0.CO;2](https://doi.org/10.1659/0276-4741(2001)021%5B0284:APITAA%5D2.0.CO;2)
- Kaçki Z, Śliwiński M (2012) The polish vegetation database: structure, resources and development. *Acta Soc Bot Pol* 81:75–79. <https://doi.org/10.5586/asbp.2012.014>
- Kaçki Z, Czarniecka M, Swacha G (2013) Statistical determination of diagnostic, constant and dominant species of the higher vegetation units of Poland. *Monogr Bot* 103:1–267. <https://doi.org/10.5586/mb.2013.001>
- Lepš J (2004) Variability in population and community biomass in a grassland community affected by environmental productivity and diversity. *Oikos* 107:64–71. <https://doi.org/10.1111/j.0030-1299.2004.13023.x>
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536. [https://doi.org/10.1890/0012-9658\(1999\)080%5B1522:GPOPIA%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080%5B1522:GPOPIA%5D2.0.CO;2)
- MacDonald D, Crabtree JR, Wiesinger G, Dax T, Stamou N, Fleury P, Gutierrez Lazpita J, Gibon A (2000) Agriculture abandonment in mountain areas of Europe: environmental consequences and policy response. *J Environ Manage* 59:47–69. <https://doi.org/10.1006/jema.1999.0335>
- Maskell LC, Firbank G, Thompson K, Bullock JM, Smart SM (2006) Interaction between non-native plant species and the floristic composition of common habitats. *J Ecol* 94:1052–1060. <https://doi.org/10.1111/j.1365-2745.2006.01172.x>
- Meiners SJ, Pickett STA, Cadenasso ML (2001) Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography* 24:633–644. <https://doi.org/10.1111/j.1600-0587.2001.tb00525.x>
- Nadolna L, Żyszkowska M (2011) Characteristics of grasslands in the Polish Sudetes in view of fodder production potential and grassland protection. *J Water Land Dev* 15:29–40. <https://doi.org/10.2478/v10025-012-0003-2>
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol Invasions* 1:3–19. <https://doi.org/10.1023/A:1010034312781>

- Planty-Tabacchi AM, Tabacchi E, Naiman RJ, Deferrari C, Decamps H (1996) Invasibility of species-rich communities in riparian zones. *Conserv Biol* 10:598–607. <https://doi.org/10.1046/j.1523-1739.1996.10020598.x>
- Poschold P, Bakker JP, Kahmen S (2005) Changing land use and its impact on biodiversity. *Basic Appl Ecol* 6:93–98. <https://doi.org/10.1016/j.baec.2004.12.001>
- Powell KI, Chase JM, Knight TM (2013) Invasive plants have scale-dependent effects on diversity by altering species–area relationships. *Science* 339:316–318. <https://doi.org/10.1126/science.1226817>
- Prévosto B, Kuiters L, Bernhardt-Römermann M, Dölle M, Schmidt W, Hoffmann M, van Uytvanck J, Bohner A, Kreiner D, Stadler J, Klotz S, Brandl R (2011) Impacts of land abandonment on vegetation: successional pathways in European habitats. *Folia Geobot* 46:303–325. <https://doi.org/10.1007/s12224-010-9096-z>
- Pyšek P, Pyšek A (1995) Invasion by *Heracleum mantegazzianum* in different habitats in the Czech Republic. *J Veg Sci* 6:711–718. <https://doi.org/10.2307/3236442>
- Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53:131–143. <https://doi.org/10.2307/4135498>
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib* 6:93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511623387>
- Ruprecht E, Nyedyi MZ, Szabó A, Fenesi A (2016) Biomass removal by clipping and raking vs burning for the restoration of abandoned *Stipa*-dominated European steppe-like grassland. *Appl Veg Sci* 19:78–88. <https://doi.org/10.1111/avsc.12199>
- Seabloom EW, Borer ET, Buckley YM, Cleland EE, Davies KF, Firn J et al (2015) Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nat Commun* 6:1–8. <https://doi.org/10.1038/ncomms8710>
- Szymura M, Szymura TH (2015) The dynamics of growth and flowering of invasive *Solidago* species. *Steciana* 19:143–152. <https://doi.org/10.12657/steciana.019.016>
- Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities. University of Chicago Press, Chicago, pp 13–25
- Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol Lett* 8:857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>
- Vilà M, Ibáñez I (2011) Plant invasions in the landscape. *Landsc Ecol* 26:461–472. <https://doi.org/10.1007/s10980-011-9585-3>
- Vilà M, Weiner J (2004) Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments. *Oikos* 105:229–238. <https://doi.org/10.1111/j.0030-1299.2004.12682.x>
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Walczak W (1968) *Sudety*. PWN, Warszawa – Kraków – Gdańsk – Łódź
- Wehn S, Taugourdeau S, Johansen L, Hovstad KA (2017) Effects of abandonment on plant diversity in semi-natural grasslands along soil and climate gradients. *J Veg Sci* 28:838–847. <https://doi.org/10.1111/jvs.12543>
- Whittaker RH (1965) Dominance and diversity in land plant communities. *Science* 147:250–260. <https://doi.org/10.1126/science.147.3655.250>
- Woś A (1999) *Klimat Polski*. PWN, Warszawa
- Young J, Watt A, Nowicki P, Alard D, Clitherow J, Henle K, Johnson R, Laczko E, McCracken D, Matouch S, Niemela J, Richards C (2005) Towards sustainable land use: identifying and managing the conflicts between human activities and biodiversity conservation in Europe. *Biodivers Conserv* 14:1641–1661. <https://doi.org/10.1007/s10531-004-0536-z>
- Zehnsdorf A, Hussner A, Eismann F, Rönnicke H, Melzer A (2015) Management options of invasive *Elodea nuttallii* and *Elodea canadensis*. *Limnologia* 51:110–117. <https://doi.org/10.1016/j.limno.2014.12.010>