



Linking the diversity of native flora to land cover heterogeneity and plant invasions in a river valley



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ABSTRACT

Plant invasions and land cover changes are two important threats to biodiversity. River valleys, which are considered as hotspots of biodiversity, have been subjected to the both threats for centuries. Here we examined the impact of river bed proximity and land cover heterogeneity on the species richness of native, red-listed and invasive plants as well as the spatial associations between the three plant groups for alpha-, beta- and gamma-diversity. Surveys were conducted in 140 plots (1 km² each) in the San River Valley (SE Poland). Our study showed that proximity to the river bed and land cover diversity was positively associated with both native and invasive plant species richness. The species richness of all three plant groups in the studied plots (alpha-diversity) was positively correlated across space. However, invasive plant species richness was negatively linked to beta- and gamma-diversity of native and red-listed species. In contrast, native plant species richness correlated neither with beta- nor with gamma-diversity of invasive species, thus, the hampering effect of high species richness on invasions was not confirmed. We conclude that studies of invasive plants should include multiple diversity levels as the effects may be hidden when evaluations are only made at the local spatial scale (alpha-diversity). Our study suggests that maintenance and restoration of forests close to the river may hamper alien plant invasions.

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1. Introduction

Alien plant invasions promoted by human activities pose a growing problem for biodiversity conservation worldwide and have been recognized as a major driver of the decline of global species diversity (Mack et al., 2000). Alien plant species can significantly alter native ecosystems by their extensive use of resources, the accumulation of litter or salt, as well as by changing disturbance regimes, hydrology and nutrient cycling (Richardson et al., 2000). As a consequence, they negatively affect the richness, diversity and composition of native communities (Hejda et al., 2009), leading to the extinction of vulnerable native species and the homogenization of floras at different spatial scales (Wilcove et al., 1998; Schwartz et al., 2006). Therefore, alien plants are able to cause great environmental damage and generate considerable economic costs (Pimentel et al., 2005). However, the mechanisms responsible for alien plant invasions and their impact on natural ecosystems are complex and not fully understood. Identifying the determinants of alien species invasiveness is a challenging task, and predicting future invasion patterns is crucial for taking effective steps to prevent the further spread of biotic invaders (Mack et al., 2000). In this respect, particularly the

issue of secondary invasions needs to be better understood (Pearson et al., 2016). Finally, increased knowledge about interactions between alien and native species at different scales is needed to mitigate the damage caused by alien plant invasions.

Also extensive changes in the land-cover seriously affect biodiversity. Deforestation, urbanization and habitat fragmentation, are directly responsible for population declines and extinctions of native species (Wilcove et al., 1998; Jetz et al., 2007). Moreover, land cover changes influence native species diversity indirectly by facilitating the dispersal of alien plants in altered environments (Blanchet et al., 2015). Considerable effort is currently devoted to assessing the risk of the spread of alien plants in various ecosystems (Chytrý et al., 2008) and to predict the impact of alien species due to future land-cover changes (Chytrý et al., 2012).

River valleys are regarded as regional hotspots of biodiversity (Naiman et al., 1993; Ward et al., 2001), but they simultaneously have undergone severe human-induced changes for centuries (Décamps et al., 1988). The land-cover within river valleys has been altered as a result of river flow regulation and drainage, agricultural expansion, extensive building development etc. Hence, an extensive loss of natural riverine vegetation has been observed, locally reaching a decrease of up to 95% of its original coverage (Tockner and Stanford, 2002). River valleys are also especially susceptible to invasions by alien plant species (Pyšek and Prach, 1995). Flowing water acts as an effective dispersal

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agent supporting the downstream movement of plant diaspores, while natural fluctuations in the water level facilitate the colonization of river valleys by alien plants (Davis et al., 2000). Currently, several legislative efforts are being implemented in order to improve the conservation of riverine ecosystems (e.g. the EU Water Framework Directive). Furthermore, over 300 conservation projects in river valleys have been co-funded by LIFE (the EU financial instrument supporting nature conservation) since 1992 (<http://ec.europa.eu/environment/life/>).

Despite the fact that invasions of alien plant species are a central threat to biodiversity, the relationships between alien and native plant species are poorly understood. Many theoretical and empirical studies suggested a negative relationship between plant diversity and vulnerability to invasions (e.g. Levine, 2000; Maron and Marler, 2008). Thus, invasions should be hampered at species-rich sites, mainly by the strong competition and domination of native species. An alternative hypothesis states that the richness of native and invasive plants are spatially synchronized by the same environmental factors (Deutschewitz et al., 2003), therefore, hotspots of native and invasive species may spatially overlap. In the case of river valleys, however, the plant diversity of native and alien species has been studied mainly in the narrow riparian zone (Renöfält et al., 2005a; Hejda and Pyšek, 2006), and few researches cover the adjacent habitats, and therefore, more studies are needed to disentangle these two alternative hypotheses concerning river valleys.

In this study, we focused on the spatial distribution of vascular plant species richness within the San River Valley (south-eastern Poland). We considered three groups of species. The first group consisted of native vascular plants. Since many alien species pose no problem from a conservation point of view, the second studied group included only invasive alien species, which might have a negative impact on native plants (Hejda et al., 2009; Pyšek et al., 2012). Invasions of alien plants sometimes impact rare species more than common ones (e.g. when common species are strong competitors compared to rare species, see Powell et al., 2011) thus the third group consisted of red-listed species. Most of the research on plant diversity patterns is on a fine-scale (the community level) or a broad-scale (the level of geographical regions), creating a gap in knowledge about the diversity pattern of the intermediate scale (Heikkinen, 1996). We therefore, focused on the meso-scale and conducted our survey using data collected in 1 km × 1 km plots. First, we investigated the impact of land cover heterogeneity, and the river bed proximity on alpha-diversity of the three studied plant groups. We expected that a high proportion of forest should favor native species, while human settlements should promote invasive alien species (e.g. Kowarik et al., 2013). Moreover, we predicted that land cover diversity and proximity to the river are positively related to the species richness of both native and invasive plants. Second, we tested whether richness of natives and invasive species was related to the beta-diversity of the remaining studied groups. Third, we investigated the variation in gamma-diversity of the three plant groups in relation to the richness of native plants and invasive plants.

2. Materials and methods

2.1. Study area

The study was conducted in the lower course of the San River Valley, which is a right-bank tributary of the Vistula River (Fig. 1a, b). The river originates in the Carpathians and is 457 km in length. The catchment area comprises approximately 17,000 km² while mean annual river discharge at the confluence with the Vistula River is 123 m³ s⁻¹ (Czarnecka, 2005). The annual growing season of this region (defined as the number of days with temperatures exceeding +5 °C) lasts 225 days (Ustrnul and Czekierda, 2003). The San River Valley comprises many natural and semi-natural ecosystems. It therefore represents a suitable system for studies of plant diversity and makes it possible to analyze a regional pattern of plant distribution. The San River Valley is also considered very important for biodiversity conservation, with the most

valuable sections protected as Special Areas of Conservation (SACs) established under Natura 2000 (an EU network of protected areas). Vegetation typical for muddy river banks, riparian shrubs and forests as well as herbaceous fringes develop along the studied section of the San River, while the rest of the valley is covered mostly by arable fields, meadows and forests.

2.2. Sampling

Ten transects were established in the study area, each placed perpendicularly to the San River bed and denoted using letters A–J. The distance between successive transects was about 15 km (Fig. 1b). Each transect was divided into 14 sampling plots (1 km × 1 km). In each transect, seven plots were situated on the left bank and seven on the right bank of the river. In total, 140 plots were studied (Fig. 1c).

Field surveys were carried out in 2009–2012. The sampling design was largely adopted from Renöfält et al. (2005b) who also explored relatively large plots. The number of vascular plant species in each plot was evaluated. One botanist (A. Nobis) took an inventory of each plot, therefore, researcher-specific subjectivity did not contribute to the differences in species lists among plots. The botanist walked along a total of eight strips (each 1 km long and c. 120 m wide) which were oriented east-west. Such a strategy enables the exploration of all habitat types. Each strip within a plot was visited four times between early spring and late autumn. The habitat patches within strips were explored until the number of species tended to saturation. Identification of plants was not always possible during field studies, thus some plant material was collected, dried and determined using the available keys. The specimens representing critical taxa were revised by specialists (see Acknowledgements).

For each plot, we calculated the number of plant species belonging to the three groups: native, red-listed and invasive species. The list of native species was prepared based on the national checklist (Mirek et al., 2002), but in the statistical analysis, red-listed species were excluded from this group. The red-listed species were determined from the national Red List (Zarzycki and Szeląg, 2006). The list of invasive species was based on a study by Tokarska-Guzik et al. (2012), who adopted a definition of invasive plant corresponding to that proposed by Richardson et al. (2000). The full lists of the three investigated groups of species are provided in Appendix A. The nomenclature of the plant species follows Mirek et al. (2002).

2.3. Statistical analyses

We calculated the distance of each plot from its center to the San River. This distance ranged from 370 m (for plots adjacent to the river bed) to 6484 m (for the most distant plots). The share of land cover classes in each of the 140 studied plots was calculated using CORINE Land Cover 2006 vector data (European Environment Agency, 2013) in GIS (ArcMap 10.1) and presented in Fig. 1c. In total, 16 land cover classes were identified in all studied plots (from 1 to 6 in each plot), but only 11 classes covered >0.5% of the plots. On the basis of the proportion of these 16 classes, we calculated the Shannon diversity index for each plot. The index ranged from 0 (homogenous plot, with one land cover class) to 0.75 (heterogeneous plot, with many classes of similar coverage). We used a principal component analysis (PCA) with varimax rotation to transform the 11 original classes with total coverage exceeding 0.5% (remaining five classes were ignored) into four orthogonal components. Associations between the four extracted components and original land cover classes are given in Table 1 (see also Fig. A1). The four extracted components, land cover diversity index and distance to the river bed were thereafter used in the statistical modeling.

The variability of plant species richness across the 140 plots (alpha-diversity) was analyzed by using generalized additive mixed models (GAMMs) with a Poisson error and log link (but quasi-Poisson and Gaussian models gave very similar results). Modeling was performed

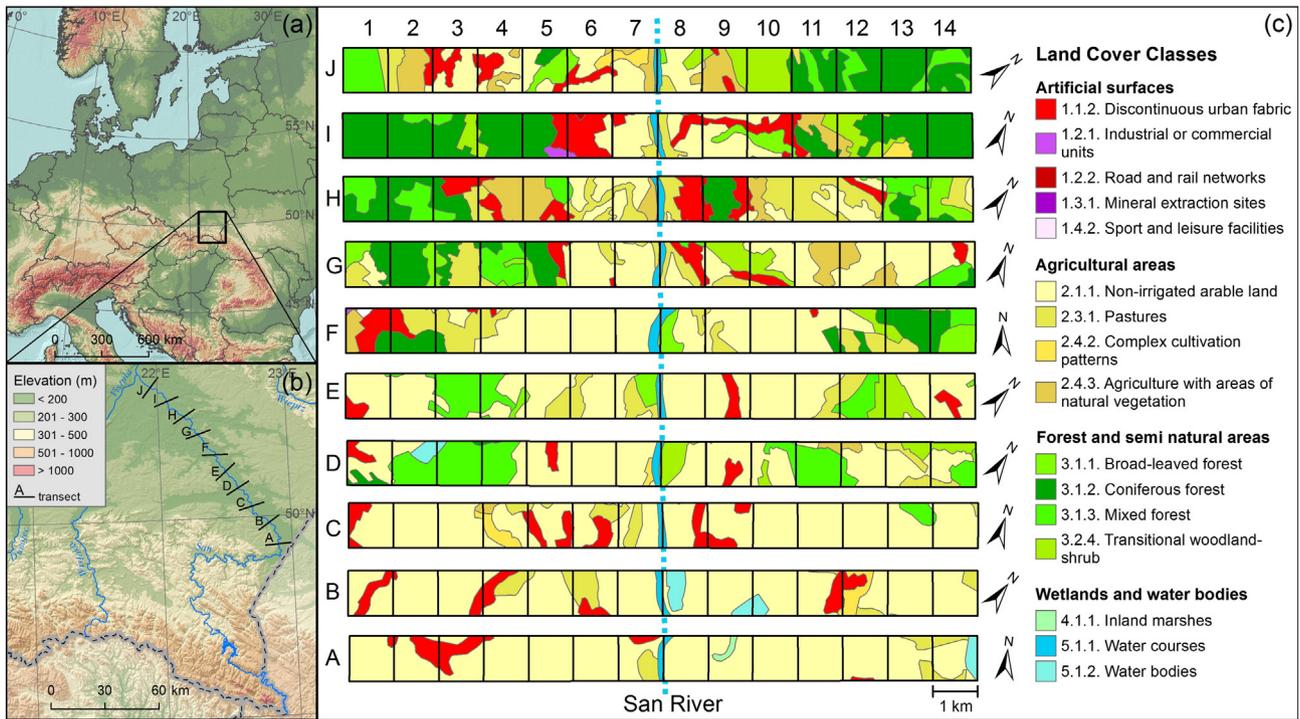


Fig. 1. Location of the study area (a, b) and land cover composition in 140 sampling plots (1 km × 1 km each) based on the CORINE Land Cover third level classes (c). For full nomenclature of particular classes see CORINE Land Cover 2006 data (European Environment Agency, 2013).

for the plant species richness of the three distinguished plant groups used as response variables: number of native species, red-listed species and invasive species. For each of these groups, a separate model was fitted (GAMM 1–3, respectively). In all three GAMMs, we used a common set of predictors: the effects of distance to the river bed and land cover diversity index were fitted using thin plate regression splines to allow for possible nonlinear effects; four PCA components (PC1–4) were fitted as covariates and transect ID was used as a random factor. Spatial autocorrelation of the data was addressed in each model by including the interaction of longitude and latitude fitted with thin plate regression splines (Wood, 2006; Dormann et al., 2007). With this procedure, part of the variation of a response variable is explained by the longitude and latitude of a given square, which makes the residuals of GAMMs spatially independent. Moreover, in GAMM1 (native), we included the species richness of invasive plants as an additional covariate. In GAMM2 (red-listed), we included the species richness of both native and invasive plants as two independent covariates, and in GAMM3 (invasive), we included the species richness of native plants as an

additional covariate. The three GAMMs were checked for the residual spatial autocorrelation with the help of Moran's I statistics computed for 10 distance classes independently for each model (30 computations in total). The Moran's I statistic did not exceed 0.07 ($p > 0.7$ for the first distance class; $p > 0.03$ in all cases) for any of the cases, confirming that there were no problems with the spatial autocorrelation. We based the parameter estimation on the full models (i.e. we did not exclude insignificant predictors) computed using the "mgcv" package (Wood, 2006) implemented in R (R Core Team, 2015).

As a second step, we investigated the beta-diversity (differences in species composition among sites) and its two independent components: nestedness (species richness loss or gain among sites where species lists from sites with smaller number of species are nested in lists of the richer sites) and turnover (replacement of one species by others; Baselga, 2010). The proportion of these components is central for understanding the impact of invasive plants on the native flora. Thus, we divided all 140 plots with respect to richness of native plants (above and below the median, providing 70 native-rich and 70 native-poor plots respectively) and the richness of invasive plants (80 invasive-rich and 60 invasive-poor plots) which resulted in 26 native-rich and invasive-poor plots, 34 native-poor and invasive-poor plots, 36 native-poor and invasive-rich plots and 44 native-rich and invasive-rich plots. Next, we calculated beta-diversity (β_{SOR}) and decomposed beta-diversity of red-listed, native and invasive plants into the two components (nestedness (β_{NES}) and turnover (β_{SIM})) for the subsets of plots (native-rich, native-poor, invasive-rich and invasive-poor – see above) using the "betapart" package (Baselga and Orme, 2012) in R. We assessed significance of the differences in beta-diversity between the subsets of plots on the basis of 1000 samples of 24 randomly selected plots (which is slightly lower than the minimum number of plots in a group and thus allowing for the variation in beta-diversity among samples, see Baselga and Orme, 2012).

Finally, we investigated whether the gamma-diversity (i.e. total species richness) of a given plant group was related to the species richness of remaining groups. We drew four rarefaction curves for red-listed plants, separately for the four possible combinations relating to the

Table 1
Principal component analysis (PCA) based on the 11 CORINE Land Cover classes computed for 140 plots (1 km × 1 km each) in the San River Valley. Loadings below 0.4 are not shown.

CORINE land cover class	Share	PC1	PC2	PC3	PC4
2.1.1. Non-irrigated arable land	50.62	-0.90			
3.1.2. Coniferous forest	11.69	0.76			
2.3.1. Pastures	8.76			0.84	
3.1.3. Mixed forest	7.87	0.47	-0.44		
1.1.2. Discontinuous urban fabric	7.70		0.75		
2.4.3. Agriculture with areas of nat. vegetation	3.88				0.64
3.2.4. Transitional woodland shrub	3.79				0.68
3.1.1. Broad-leaved forest	2.77	0.40			-0.45
5.1.1. Water courses	1.10			0.49	
2.4.2. Complex cultivation patterns	0.87				
5.1.2. Water bodies	0.71		-0.47		
Proportion of variance		0.17	0.12	0.11	0.11
Cumulative variance		0.17	0.29	0.40	0.51

abundance of native species (native-poor and native-rich plots) and the abundance of invasive species (invasive-rich and invasive-poor plots). Next, we drew two rarefaction curves for native plants (separate for invasive-rich and invasive-poor plots) and two curves for invasive plants (native-rich and native-poor plots). We performed sample-based rarefaction, including unconditioned 95% CI using the 'iNEXT' package (Hsieh et al., 2014) in R.

3. Results

3.1. Alpha-diversity

The total number of species noted in all studied plots was 967. From 183 to 409 vascular plant species were recorded in a single plot (266.3 on average, ± 40.5 SD). Twenty plots adjacent to the San River bed host 68% of all vascular plant species noted in the investigated transects. We found 777 native species in the study area, from 129 to 330 per plot (209.3 on average, ± 34.9 SD). We found 32 red-listed species. Red-listed species were found in 124 plots and the largest number of red-listed species in a particular plot was 7. Among 190 recorded alien species, 47 are considered to be invasive in Poland. A single plot harbored from 8 to 28 invasive species (18.7 on average, ± 4.3 SD). The species richness of the three distinguished groups in the studied plots were positively correlated (native with invasive species: $r = 0.21$, $p = 0.0115$; red-listed with invasive species: $r = 0.28$, $p = 0.0006$; red-listed with native species: $r = 0.25$, $p = 0.0025$).

Predictors explained about half of the variation in species richness of the three groups in the 140 plots (Table 2). The richness of native species was positively linked with the proximity to the river bed and land cover diversity (Table 2, Fig. 2), but poorly linked with landscape composition. Only the proportion of pastures and water courses (PC3) was weakly positively correlated with the species richness of native plants (Table 2).

The higher richness of red-listed species was mainly associated with high proportions of arable land (PC1), but increasing proportions of pastures, watercourses (PC3), shrubs and agricultural areas characterized by a significant share of natural vegetation (PC4) were also positively linked with the richness of red-listed plants (Table 2). The species richness of red-listed plants was not correlated with land cover diversity, but it tended to be higher close to the river bed (Table 2, Fig. 2). The richness of red-listed species was positively associated with the richness of native species, and negatively with the richness of invasive species (Table 2).

The richness of invasive species was positively linked with the proportion of arable land (PC1), urbanized areas (PC2), shrubs and agricultural areas characterized by a significant share of natural vegetation (PC4). Proportions of forests (PC1) were negatively associated with the richness of invasive species. Land cover diversity and proximity to the river bed had positive effect on the richness of invasive species. (Table 2, Fig. 2).

3.2. Beta-diversity

Beta-diversity of red-listed plants and native plants was significantly lower in invasive-rich plots compared to invasive-poor plots. However, beta-diversity of both red-listed plants and invasive plants was not associated with richness of native plants (Fig. 3, upper panel).

For all three studied plant groups, the spatial turnover of species was responsible for ca. 70–95% of the overall beta-diversity. However, the contribution of turnover-diversity in the overall beta-diversity was clearly lower in the case of red-listed species (ca. 70–80%) compared to native species (over 90%). In the plots with relatively many invasive species, the proportion of the beta-diversity explained by turnover was lower for both red-listed and native plant species. About 85% of invasive plant beta-diversity was attributed to turnover and this proportion was not correlated with native plant richness (Fig. 3, lower panel).

3.3. Gamma-diversity

Gamma-diversity patterns analyzed with the use of rarefaction showed that the total red-listed species richness depended on both the richness of native and invasive plants. There was a higher gamma-diversity of red-listed plants for the subsets of plots with few invasive species compared to plots with many invasive species. Simultaneously, a higher gamma-diversity of red-listed plants was noted for the subsets of plots with many native plants compared to plots with few native plants (Fig. 4). The cumulative number of native plant species was significantly lower for the subset of plots with relatively high species richness of invasive plants compared to plots with relatively few invasive plants (Fig. 4). In contrast, the gamma-diversity of invasive plants tended to be higher for the subset of plots with a relatively high species richness of native plants, although the 95% confidence intervals overlapped, at least for the sample size exceeding 15 plots (Fig. 4).

4. Discussion

Following our predictions, proximity to the river bed was positively associated with both native and invasive species richness. A similar tendency was also recorded for red-listed species. All these groups were influenced by the land cover composition (PC1–4), although in different ways. Land cover diversity, however, was positively associated with native and invasive species richness. The richness of invasive plants was negatively linked with the alpha-, beta- and gamma-diversity of red-listed plants as well as beta- and gamma-diversity of native species, while the richness of native plants was positively associated with the alpha- and gamma-diversity of red-listed species. However, contrary to the predictions, the species richness of native plants did not correlate negatively with diversity of invasive plants at any level. Below we discuss the possible mechanisms driving the observed patterns.

Table 2
Summary of generalized additive mixed models explaining the species richness of native, red-listed, and invasive plants in relation to land cover composition (PC1–4), land cover diversity index and distance to river. Significant effects are marked in bold, estimated degrees of freedom (Edf) are given for spline fits.

Predictor	Native		Red-listed		Invasive	
	B (SE)	p-Value	B (SE)	p-Value	B (SE)	p-Value
Intercept	5.267 (0.063)	0.0000	−0.460 (0.508)	0.3667	2.779 (0.121)	0.0000
Native	–		0.009 (0.002)	0.0000	0.001 (0.000)	0.2644
Invasive	0.004 (0.003)	0.2709	−0.042 (0.018)	0.0194	–	
PC1 (arable-forest)	0.001 (0.014)	0.9561	−0.418 (0.088)	0.0000	−0.073 (0.020)	0.0004
PC2 (urban-water)	−0.010 (0.011)	0.3251	0.099 (0.056)	0.0818	0.047 (0.014)	0.0010
PC3 (pasture, water)	0.024 (0.011)	0.0299	0.184 (0.059)	0.0023	0.009 (0.016)	0.5635
PC4 (shrub-forest)	−0.009 (0.010)	0.3413	0.166 (0.055)	0.0034	0.041 (0.013)	0.0022
Spline (land cover diversity)	Edf = 1.000	0.0000	Edf = 1.000	0.2270	Edf = 1.000	0.0062
Spline (distance to river)	Edf = 1.000	0.0187	Edf = 1.000	0.0754	Edf = 1.000	0.0000
R ² adjusted	0.561		0.442		0.551	

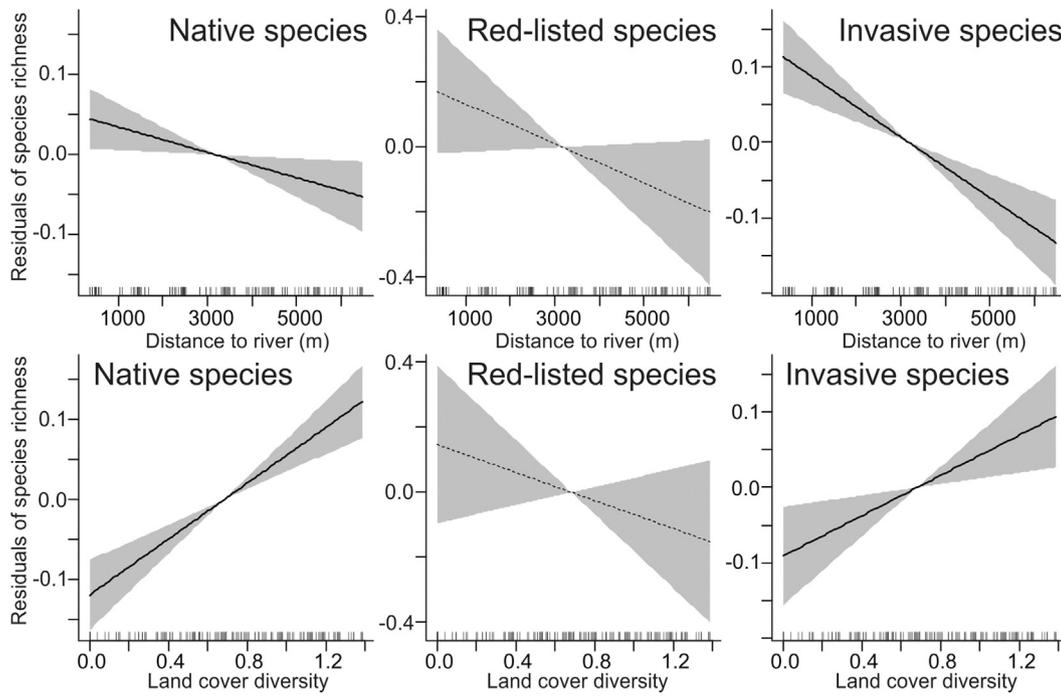


Fig. 2. The effects of distance to river bed and land cover diversity on the species richness (i.e. alpha-diversity) of native, red-listed, and invasive plants of plots in the San River Valley as predicted by GAMMs presented in Table 2. Non-significant effects are shown with dashed lines, 95% CI are marked with gray polygons.

4.1. Environmental factors

The positive association between proximity to the river bed and the species richness of both native and invasive plants was recorded despite the fact that land cover composition and land cover diversity were also included in the models. We have two explanations for this pattern. First, plots adjacent to the San River bed include most of the habitats common

in the study area as well as those restricted to riparian zones (river banks, watercourse veils, etc.). Such small-scale habitats not included in the CORINE maps boost overall species richness. Second, natural disturbances caused by flooding as well as hydrologic connectivity can also positively affect species richness in the vicinity of the river bed (Planty-Tabacchi et al., 1996; Ward et al., 2002). Consequently, plots located by the river bed included almost 70% of all species noted in the

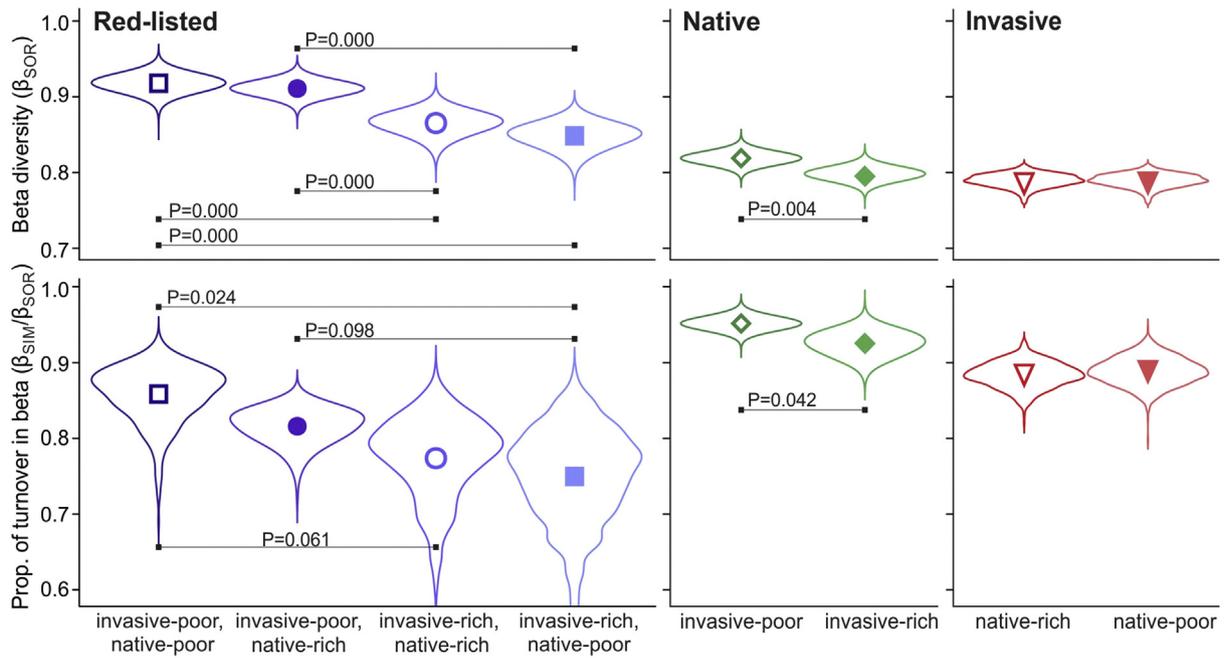


Fig. 3. Changes in overall plant beta-diversity (β_{SOR} , upper panel) and the proportion of the turnover-resultant beta-diversity in the overall beta-diversity (β_{SIM}/β_{SOR} , lower panel) calculated for the subsets of plots in the San River Valley divided into categories based on richness of invasive and native species (see x-axis classes in each graph). The distribution of the re-sampled proportion is based on 1000 samples of 24 plots and is shown with kernel density curves. Mean values are marked with different symbols. Significance of the differences is shown when $p < 0.1$.

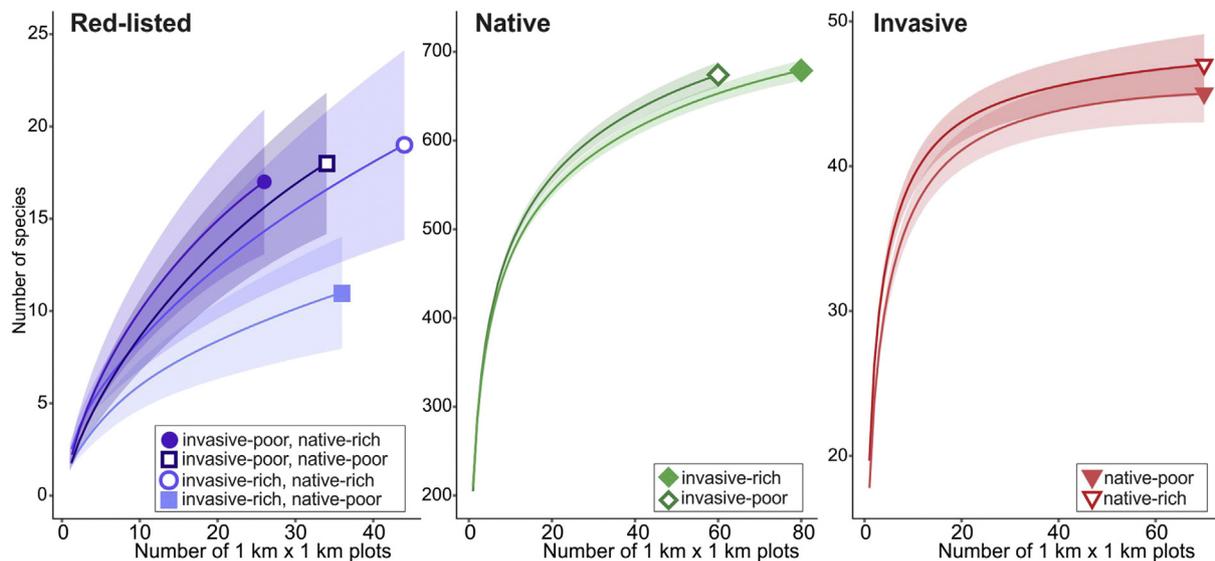


Fig. 4. Expected cumulative number of species (i.e. gamma-diversity) for the three studied groups of plants (with 95% CI marked as transparent polygons) as a function of the number of 1 km × 1 km plots in the San River Valley with high or low numbers of native and invasive plant species (following the legends in each graph).

investigated transects. Therefore, our results are consistent with previous studies showing that riparian zones are extremely rich in species (Naiman et al., 1993) and species richness decreases with the distance to the river (Heikkinen, 1996).

Many studies show a positive association between spatial environmental heterogeneity and species richness (e.g. Hortal et al., 2009 but see Allouche et al., 2012 for other patterns). In our study, the richness of native species was poorly explained by land cover composition, whereas the richness of invasive plants was positively linked to the proportion of land cover classes with substantial human activities. This seems to confirm that anthropogenic disturbances facilitate the dispersal of alien species directly or by providing environmental conditions favored by invaders (Planty-Tabacchi et al., 1996; Gavier-Pizarro et al., 2010; Gassó et al., 2012). On the other hand, our results seem to contradict earlier findings that the richness of native and alien plants benefit from the same land cover categories (Deutschewitz et al., 2003). The importance of PC1 (gradient between arable land and forests) for red-listed species might seem surprising, but 9 of all 32 red-listed species noted in the study area are weeds endangered due to the intensification of agriculture (e.g. *Kickxia elatine*, *Lythrum hyssopifolia*, *Valerianella locusta* see Appendix A). Land cover diversity positively affected native and invasive plant species richness. This finding follows a general rule confirmed by the recent meta-analysis of data from studies worldwide (Stein et al., 2014).

4.2. Spatial associations between studied plant groups

Small-scale studies have usually indicated a negative spatial relationship between invasions and species richness (e.g. Tilman, 1997; Naeem et al., 2000), whereas large-scale observations revealed positive relationships between native and alien plant species richness (Planty-Tabacchi et al., 1996; Deutschewitz et al., 2003), thus the relationship between invasive and native species depends on the size of the sampling plot (Powell et al., 2011). Such a dependence was also confirmed for riparian areas by Brown and Peet (2003), who found a positive relationship between the species richness of native and alien species for 100 m² plots and a negative relationship for 0.01 m² plots. Our studies confirmed positive correlations between the native and invasive plant species richness, which is a plausible result considering the size of studied plots. However, more detailed analyses using land cover data revealed that the conclusions derived from such simple correlations may be misleading.

The positive association between the diversity of native and red-listed plants, at both the alpha- and gamma-level, was observed despite the fact that these two groups responded rather differently to land cover heterogeneity. This result can be driven by the large size of the sampling plots because in large plots there is more room for co-occurrence among ecologically different species. At the same time, invasive species richness appeared to be independent on native species richness. We therefore cannot confirm the hypothesis about the hampering effect of diversity on invasions (Elton, 1958). Our results suggest that land cover transformation, flooding disturbances and the supply of diaspores by flowing water are much stronger drivers of invasions in river valleys compared to hypothetical interactions with the native flora.

The diversity of invasive plants was negatively linked to the richness of red-listed species at the alpha-, beta- and gamma-level, and to the richness of natives at the beta- and gamma-level. Moreover, in invasive-rich plots, species turnover among plots was proportionally lower for both red-listed and native plants, while the contribution of nestedness to the overall beta-diversity was higher. The higher proportion of nestedness-resultant diversity in the overall beta-diversity may suggest that species losses or gains among plots are more important in plots experiencing invasions (Si et al., 2015). All these negative associations may result from biotic interactions e.g. competition for common resources (especially strong in *Acer negundo*, *Padus serotina*, *Reynoutria japonica*), overgrowing (*Echinocystis lobata*), reduced availability of pollinators (*Impatiens glandulifera*) or allelopathy (*Robinia pseudoacacia*, *Solidago gigantea*). Some of the rare species are weak competitors (Kunin and Gaston, 1993; Rünk et al., 2004), thus invasions may impact red-listed plants more severely than common ones, which is supported by our analyses. Moreover, we recorded slightly different patterns of species distribution among the plots in the case of red-listed and native plants. Generally, beta-diversity was mainly driven by species replacement (turnover), which may suggest that competitive interactions between species are important (Baselga, 2010; Socolar et al., 2016) but other drivers of such pattern, e.g. environmental filtering, cannot be excluded.

5. Conclusions

Our study showed clearly the scale-dependence of the relationships between richness of native and invasive plants. The spatial co-occurrence of the species richness of native and invasive plants locally (i.e. alpha-diversity) suggests positive associations (simple correlations) or

no associations with positive tendency (models incorporating detailed environmental data). Our study shows therefore that hotspots of native species in river valleys are simultaneously the most invulnerable. Thus, conservation strategies of riverine biodiversity need to take this co-occurrence into account by adjusting conservation measures. However, scaling-up the patterns to beta- and gamma-levels shows a negative relationship between invasive and native (or red-listed) species. Moreover, the proportion between nestedness-resultant and turnover-resultant components of beta-diversity also changes. We show, therefore, that the effects of invasions can be distinct at larger spatial scales but overlooked when investigations are only made at local scales. This stays in line with the recent recommendations of Socolar et al. (2016) that we need a deeper understanding of human impact on beta-diversity for interpreting alpha-scale studies.

Invasions in river valleys are strongly related to land cover composition. Maintenance and restoration forest coverage close to the river in combination with reducing the coverage of urbanized and arable land may hamper invasions. We therefore suggest more careful evaluation of current flooding management, which in its present form in Poland and many other countries, leads to the deforestation of floodplains to facilitate water flow and thus may promote the spread of invasive plants.

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Appendix A. Supplementary data

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