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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 km^2 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.

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 km^2 while mean annual river discharge at the confluence with the Vistula River is 123 m^3 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