



## Research Paper

# Do levees support diversity and affect spatial turnover of communities in plant-herbivore systems in an urban landscape?



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## ABSTRACT

Valuable habitats in various spatial configurations are essential for maintaining biodiversity across highly fragmented urban landscapes. In a large-scale study, we explored the value of human-made structures – river levees – as valuable habitats that support large populations of plants and butterflies and affects the spatial turnover of species within an urban landscape. The most significant environmental variables affecting plant and butterfly populations on levees were also examined. The richness of native plant species was about 25% greater on levee transects than on control grassland transects. However, the richness and abundance of butterflies on levees were the same as on grassland sites. Among environmental factors, urban area cover negatively affected the richness of native plant species. Shrub cover decreases the richness and abundance of butterfly species. In addition, high mowing intensity had a negative influence on abundance. Community dissimilarity of plants on levees was affected by spatial variables. Our study is the first to highlight levees as significant habitats for plant and herbivorous insect persistence, and their potential function for plant dispersal.

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## 1. Introduction

Increasing urbanisation is one of the main factors negatively affecting plant-herbivore systems worldwide (Harrison and Winfree, 2015; McKinney, 2006; Palik et al., 2005). Urban areas are characterised by intensive management, with diminishing semi-natural habitat patches separated from each other by a matrix of developed features (McKinney, 2008). Thus, conservation strategies which counteract urbanisation should take into account the preservation of valuable habitats, as well as spatially affected processes such as species dispersion. Accordingly, interventions in urban landscapes, i.e. creating green areas, have been proposed in the hope that such spaces may serve as valuable habitats for living creatures (Hunter and Hunter, 2008). A further potential ben-

efit of green areas is that they may sustain spatially dependent processes (Haddad and Tewksbury, 2005), especially in the highly modified urban landscape. However, conservation of species diversity and sustaining spatial processes faces many practical hurdles. For example, landscape management in a city is costly (Commission for Architecture and the Built Environment, 2006), while its effectiveness depends on the ecological group or order of organisms being targeted (Jarošík et al., 2011) and type of matrix or landscape structure (Soga and Koike, 2013). A supplementary solution is to discover and utilise the potential advantages of existing human-made habitats and structures enriching biodiversity and enabling essential spatial connections between populations (Lenda et al., 2012; Schriever et al., 2009; Tonietto et al., 2011). For example, linear elements of the landscape, frequently related to human activity, might offer significant conservation benefits (Bueno et al., 1995; Moroń et al., 2014). Thus, environments resulting from the development of civilisation might partly reduce the adverse effects of urbanisation.

Humans traditionally settled along rivers, which led to the development of towns and cities in such places (Kostof, 1992). In developed countries, levees are built to protect urbanised areas against floods, especially since cities were usually located on river

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banks. For example, the overall length of levees in France, Poland or the USA amounts to 10 000 km, 8 500 km and 40 000 km, respectively (Dupray et al., 2010; McCully, 2007; Ministerstwo Środowiska, 2010). This shows that levees are frequent elements of the urban scenery. These and other elongated structures might be significant reproductive habitats and dispersal routes for many organisms (Fukamachi et al., 2005; Martin et al., 1991). Despite the ubiquity of levees in the landscapes of many European and American cities, their benefits for the dynamics of an urban ecosystem have not been studied to date. We therefore performed a large-scale study to explore the value of this habitat in plant-herbivore systems, i.e. native plants (hereafter plants) and butterflies in an urban landscape. To this end, we investigated the richness and abundance of plant and butterfly species, and the relationships between these groups' dissimilarities and geographic distances. In reference to biodiversity and the spatial processes at levees, we studied species richness, and abundance and dissimilarity in typical plant and butterfly habitats in urban landscapes consisting of extensively managed or recently abandoned grasslands (Skórka et al., 2007). We anticipated that, if levees are valuable habitats, they would support a richness and abundance of plant and butterfly species relatively equivalent to or even higher than on control grasslands. Next, we determined site as well as landscape variables impacting the richness and abundance of butterflies and the richness of plants on levees, in order to formulate proposals essential for improving the management of this habitat. We expected also that, if dispersal-dependent processes do not drive plant and butterfly communities, the study sites should exhibit a spatially random pattern of dissimilarity. However, if the plants and butterflies disperse using levees, this should be reflected in less dissimilar species composition at adjacent sites.

## 2. Materials and methods

### 2.1. Study area

The investigation was performed along a levee system in the agglomeration of Kraków, southern Poland (Fig. 1). Residential population density at the study area (based on the principal unit of administrative division) was 1 558 per km<sup>2</sup>, whereas for Poland it is 123 per km<sup>2</sup>. All the levees are well-settled and were constructed more than 20 years ago. We selected 30 levees and 20 grasslands in such a way as to ensure an average distance between all sites of each type as similar as possible (Fig. 1). The mean distance between all pairs of selected levees was 7.0 km (range: 0.7–20.4 km) and the mean distance between all pairs of grasslands was 6.9 m (0.6–20.6 km; Wilcoxon test,  $W = 42066$ ,  $p = 0.722$ ). The levees closest to each other were separated by a mean distance of  $1.1 \pm 0.7$  km (0.7–3.8 km), and the grasslands closest to each other were separated by a distance of  $1.3 \pm 0.6$  km (0.6–2.4 km; Wilcoxon test,  $W = 379$ ,  $p = 0.120$ ). We chose grasslands in close proximity to a levee, with the median distance to the nearest levee at 1.1 km (range: 0.6–2.7 km), in order to ensure that local environmental conditions such as bedrock, microclimate and landscape were as similar as possible to the levees. Grasslands were situated close to watercourses to minimise the potentially confounding effect of waterbody presence near levees. The levees and grasslands are both maintained with low-intensity management, with mowing taking place at most once per year.

### 2.2. Plant and butterfly surveys

The number of plant species was noted in two rectangular plots of 12 m<sup>2</sup> (3 × 4 m) situated at each site, with a short axis oriented along the nearest watercourse (Appendix A in Supplementary

**Table 1**

Variables measured on levees. Mean ± standard deviation (SD) with minimum and maximum values are shown.

Independent variables	Mean ± SD (min.–max.)
arable land cover (%)	2.41 ± 4.02 (0.00–13.91)
human settlement cover (%)	25.30 ± 22.94 (0.00–81.00)
levee cover (%)	4.13 ± 2.07 (0.30–9.67)
index of mowing frequency	0.08 ± 0.07 (0.00–0.20)
species richness of non-native plants (no. species)	4.03 ± 2.22 (0.00–10.00)
angle of slopes (degree)	25.68 ± 4.20 (16.50–38.17)
length of slopes (m)	7.22 ± 2.26 (3.58–13.17)
shrub cover (%)	11.17 ± 27.03 (0.00–100.00)
water reservoir cover (%)	11.70 ± 9.54 (0.00–34.38)
woodland cover (%)	9.92 ± 7.34 (0.00–25.34)

material). For levees, a single plot was established in the middle of the inner as well as the outer sides. There was a distance of 100 m between two plots both at levee and grassland sites. Plants were noted on three occasions, in the middle of May, at the end of June and in August.

A transect of 200 m was used at each site for butterfly surveys (Pollard and Yates, 1993). Transects at levees and grasslands were situated along the nearest watercourse. For levees, half of a transect spanned the inner side of the levee and the second half was placed at the outer side (Appendix A in Supplementary material). Butterflies were counted on each transect in May, at the turn of June and July and in August. Transects were visited in random order at different times of day and during warm and calm weather.

### 2.3. Environmental variables measured for levees

Environmental variables likely to affect native plants and butterflies were determined for levees. Those variables were arable land cover, human settlement cover, levee cover, index of mowing frequency, species richness of non-native plants, angle of slopes, length of slopes, shrub cover, water reservoir cover and woodland cover (Table 1). Shrub cover was measured as percentage (0–100%) of levee area. Arable land, human settlement, levee, water reservoir and woodland covers were measured as percentages (0–100%) in a buffer of 200 m around the transects (Appendix A in Supplementary material). Variables within buffers were measured in the field by GPS, and digitalised using the QGIS programme. Angle (degree) and length (m) were measured at both ends and in the middle of transects and then the mean was calculated. Invasive plant species were counted on the same plots that were surveyed for native plants. During each transect survey, mowing frequency was noted and the index introduced by Valtonen et al. (2006) was used. The index tallies the overall impact of mowing on plants during the study duration. For each survey a mowing intensity value (0 = no mowing, 1/2 = partial mowing, 1 = total mowing) was assigned and the value was decreased to the lower level, respectively from 1 to 1/2 and from 1/2 to 0, seven weeks after mowing, as a result of vegetation recovery after mowing. The sum of the values from each survey was used for further analysis.

### 2.4. Analysis

Model selection procedure based on information theory (Burnham and Anderson, 2002) was used to identify environmental variables associated with the richness and abundance of species on levees. For identification of the most parsimonious models from each variable set, the Akaike information criterion corrected for small sample size (AICc) was used. Next, all models were ranked according to their  $\Delta$ AICc values, and we used those with the lowest AICc combined with related weight values as the best for explaining the data. Models with  $\Delta$ AICc lower than two were acknowl-

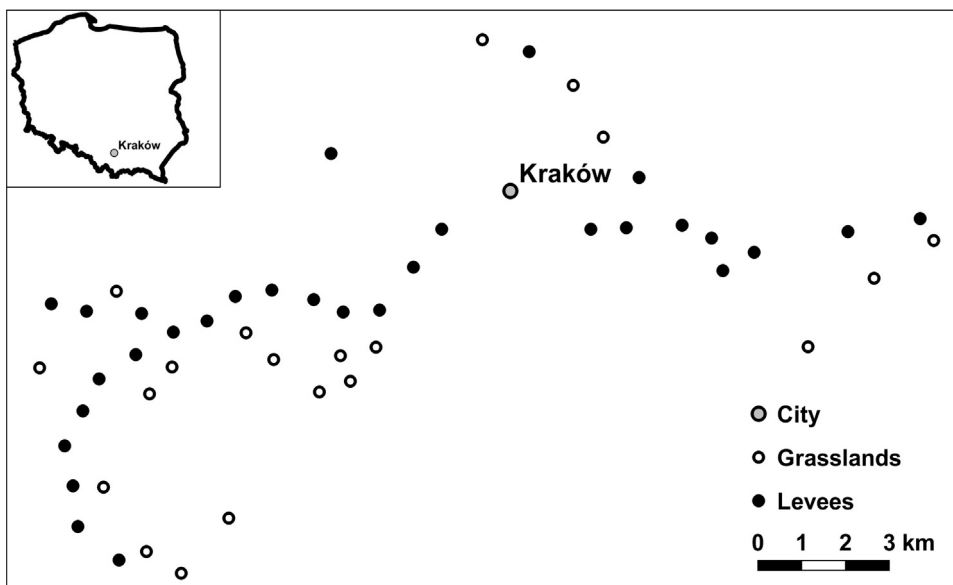


Fig. 1. Map indicating the locations of the study sites in the Kraków region, south-eastern Poland.

edged as equally good (Burnham and Anderson, 2002). Estimation of function slopes of parameters of concern was performed by model averaging (Burnham and Anderson, 2002). Lastly, the model weights were applied to determine the relative importance of each independent variable over the full set of models assessed by summing weight values of all model sets that included the independent variable of concern (Burnham and Anderson, 2002). The function slopes (betas) were considered as significant if their 95% confidence intervals did not overlap with zero. For the model selection procedure, dependent variables were square-root transformed in order to linearise relationships, to normalise distributions, and to lower the impact of outliers (Quinn and Keough, 2002). To permit detection of straightforward relationships of function slopes between independent variables, they were standardised (mean of zero and a standard deviation of one; Quinn and Keough, 2002). Spatial autocorrelation in the number of species (plants and butterflies) and individuals (butterflies) were checked by calculating Moran's statistics on correlograms (Legendre and Legendre 1998). However, there was no evidence for statistically significant autocorrelation, and therefore we used traditional statistics. Statistical models were built independently for plants and butterflies (models tested: plants – 511; butterflies – 2 047). Model selection and averaging based on the AICc were performed using SAM 4.0 software (Rangel et al., 2010). The Wilcoxon rank sum test in R (R Development Core Team, 2016) was applied to compare the number of plant species and butterfly species, as well as abundances between levees and control grasslands.

We used the Jaccard dissimilarity index to ascertain spatially affected species turnover. This index takes into account the species that are different between a pair of sites, and is defined as the proportion of the overall pull of species present at each site. The index ranges from 0 for identical pull of species at sites to 1 for no common species between sites. The Jaccard index accounts for dissimilarity derived from turnover (species replacement) as well as from nestedness (elimination of species; Baselga 2012). We used the Jaccard dissimilarity component based solely on species turnover (Baselga et al., 2013). This dissimilarity index was computed for each pair of sites for plants and butterflies.

We generated the spatial variables using Moran's Eigenvectors Maps (MEM) from the site coordinates (Borcard et al., 2011). Each spatial variable generated represents a different spatial pattern

that might explain community dissimilarity. We used all the MEM eigenvectors with positive eigenvalues as potential spatial predictors (Borcard et al., 2011). Eigenvectors with positive eigenvalues correspond to positive spatial correlation (Borcard et al., 2011). MEM eigenvectors with high associated eigenvalues, e.g. MEM1, are said to represent broad-scale patterns, whereas the MEM eigenvectors with lower associated eigenvalues, e.g. MEM7, represent finer spatial scales (Borcard et al., 2011). Next, we selected the best MEM eigenvectors explaining community dissimilarities by forward selection. The selected MEM eigenvectors were used as spatial explanatory variables. Then, with the help of partial Redundancy Analysis, we evaluated the contribution of selected MEM eigenvectors to the dissimilarity of plants and butterflies. We accounted here for the variance explained exclusively by spatial variables (after removing the confounding effect of the environmental variables). All spatial analysis was performed separately for butterflies and plants at levees and grasslands. All statistical analysis of dissimilarity was performed using the *adespatial* (Dray et al., 2016), *betapart* (Baselga, 2012) and *vegan* (Oksanen et al., 2013) packages in R (R Development Core Team, 2016).

### 3. Results

#### 3.1. Comparison of levees and grasslands

A total of 179 plant species and 40 butterfly species were recorded on levees, compared to 148 plant species and 39 butterfly species on control grasslands (Appendix A in Supplementary material). The richness of native plant species was about 25% greater on levee transects than grassland transects (28.9 vs. 21.2 species;  $W = 135.5$ ,  $p = 0.001$ ), whereas the richness of invasive species did not differ between habitats (4.0 vs. 3.3 species;  $W = 238$ ,  $p = 0.218$ ). Differences between levees and grasslands for the richness and abundance of butterfly species were not significant (9.8 vs. 10.2 species;  $W = 258$ ,  $p = 0.408$ ; 31.7 vs. 27.2 individuals;  $W = 244$ ,  $p = 0.271$ ). Altogether, 74 plants (out of 222) and eight butterflies (out of 47) were unique to levees. A total of 43 plant and seven butterfly species were unique to grasslands (Appendix A in Supplementary material). However, these differences were not significant (plants:  $F$  exact,  $p = 1.000$ ; butterflies:  $F$  exact,  $p = 0.570$ ). There were 105 species of plants and 32 species of butterflies that were present on

both levees and grasslands (Appendix A in Supplementary material).

### 3.2. Levee characteristics affecting species richness and abundance

Model selection based on Akaike's criterion identified three best models and explained about 36% of variation in native plant species richness on levees (Table 2). Among the variables we examined, only human settlement cover was displayed in all the best models (Table 2; Appendix A in Supplementary material). The species richness of plants was also affected by arable land and levee cover (Tables 2 and 3). According to Akaike's criterion, nine best models explained about 56% of the variation in species richness of butterflies (Table 2). Of the variables, shrub cover was displayed in all the best models (Table 2; Appendix A in Supplementary material). The abundance of butterflies was also affected by arable land cover, human settlement cover, index of mowing frequency, angle of slopes, length of slopes, and woodland cover (Table 3). Model selection according to Akaike's criterion showed six best models explaining about 50% of the variation in butterfly abundance (Table 2). Among the variables, the mowing index was displayed in all selected models (Table 2). The abundance of butterflies was also vulnerable to human settlement cover, species richness of native plants, angle of slopes, length of slopes, and shrub cover (Table 3).

### 3.3. Plant and butterfly dissimilarity and spatial processes

Community dissimilarity of plants and butterflies on levees and control grasslands displayed differences connected with spatial variables. Plant dissimilarity on levees was influenced by MEM1, MEM3, MEM4 and MEM5 eigenvectors: the closer the sites, the more similar their community composition ( $F_{4,15} = 1.16$ ;  $R^2_{adj} = 0.08$ ;  $p = 0.021$ ). In contrast, dissimilarity was not adjusted with spatial variables for plant species on grasslands. Spatial variables were not affected for butterflies on levees or grasslands.

## 4. Discussion

Despite the ubiquity of levees and their potential role as urban matrix habitats for the dispersion of organisms, they have never been studied in the context of plant-herbivore systems. Our results indicate that river levees are important habitats for plant and butterfly populations and that they can spatially modify dissimilarity of communities. The potential role of levees as valuable habitats may be due to the advantageous conditions and resources they offer for many species, for example, by creating a strong environmental gradient, e.g. in moisture (Moróñ et al., 2014). Also, levees cross the natural-urban gradient and thus may ensure connectivity between populations from different landscapes (Moróñ et al., 2014). However, our analysis indicated associations between spatial variables and community composition only for plants across levees. Thus, levees may have limited value for butterfly population connectivity in urban settings. This may result from the possibility that levees are very good habitats for the studied organisms. It was demonstrated that poor-quality habitats are the most effective dispersal routes because organisms are not willing to reproduce there (Haddad and Tewksbury, 2005).

### 4.1. Levees vs. grasslands

Levees are linear habitats that exhibit drier, warmer conditions at their upper portions whereas their lower segments are colder and wetter, creating a strong environmental gradient. Moreover, floods and regular disturbance at the time of repairs often add to

the considerable habitat mosaic (Fies et al., 2016). Thus, levees contain valuable habitats for many species in plant-herbivore systems, particularly in anthropogenic landscapes. The results show that levees are significant habitats for plants and butterflies in an urban landscape. The mean number of plant species was significantly higher compared to control grasslands, and the mean number of butterfly species and individuals did not differ between levees and grasslands. This indicates that the richness of plant species is not necessarily a good indicator of butterfly richness between levees and grasslands (Kremen, 1992).

### 4.2. Levee characteristics affecting plants and butterflies

The environmental attributes of levees significantly affected the richness of plant species. The factors explained about 36% of variation in plant composition on levees. The most important factor for the richness of plant species on levees was human settlement cover. Many studies about the response of plant communities to urbanisation have found that richness increases with only moderate urbanisation, decreasing when intensity is low or high (McKinney, 2008). However, we only found a strong linear, negative relationship between plant richness and human settlement cover. Despite this, our results are in line with many studies showing the negative impact of human settlements on plants (McKinney, 2008). Urbanisation negatively affects plant populations because it causes a significant increase in disturbance, structural simplification of the remaining vegetation, and increased pollution (McKinney, 2008). These factors combine to decrease habitat area and quality for plants. Moreover, the effects of these factors seem to boost their magnitude along with urbanisation level (McKinney, 2008).

The environmental attributes of levees also significantly affected the richness and abundance of butterfly species. The factors explained about 56% of variation in butterfly species and 50% of variation in abundance on levees. The most important factor shaping the diversity of butterflies, and other pollinator species, is foraging requirements (Potts et al., 2005). Native plant species at levees did not influence the richness of butterflies in our study area. This may be the consequence of mobile species, such as some butterflies, using resources over a broader area, not only at the scale of a levee, notably in intensively modified landscapes (Ekroos and Kuussaari, 2011). Shrubs negatively impact butterfly species and their abundance. Dense stands of shrubs could lower the appropriateness of levees for pioneer or specialist butterfly species by, for example, altering the composition of food plants. The presence of shrubs might also cause greater predation rate by birds of woodlots that hunt butterflies (Lenda and Skórka, 2010). Finally, mowing frequency seems to be a factor that negatively impacts the abundance of butterflies on levees. This finding is in line with earlier studies on other linear habitats, indicating the direct negative impact of mowing on food resources and modification of vegetation structure (Skórka et al., 2013; Valtonen et al., 2006).

### 4.3. Effects of levees on species turnover

Distance decay of turnover for plants and invertebrates has already been demonstrated (Nekola and White, 1999; Rouquette et al., 2013). However, no studies have examined plant species turnover in plant-herbivore system along levees in a highly altered urban landscape. It is known that, in a patchy urban area, linear habitats facilitate movements of plants and animals between sites (Beier and Noss, 2008). However, the conservation value of corridors has also been questioned (Good, 1998). Because evidence from rivers as dispersal routes for terrestrial organisms is limited (Rouquette et al., 2013), the role of levees in enhancing the dispersal of species was also barely known (Frey and Conve, 2006). Our results show that levees affected spatially turnover for

**Table 2**  
Best models characterizing plant or butterfly species richness and abundance by variables on river levees. For each model the number of predictors (k), variance explained by the model ( $r^2$ ), the Akaike information criterion score (AICc), the difference between the given model and the most parsimonious model ( $\Delta$ ) and Akaike weight (w) are listed. Explanations of variable codes: arable land cover – arable, human settlement cover – human, levee cover – levee, index of mowing – mowing, species richness of native plants – native, species richness of non-native plants – non-native, angle of slopes – angle, length of slopes – length, shrub cover – shrub, water reservoir cover – water, woodland cover – wood. (↑) – positive statistically significant relationship; (↓) – negative statistically significant relationship.

No.	Model	k	$r^2$	AICc	$\Delta$	w
<b>Plant species richness</b>						
1	human (↓)	1	0.35	202.43	0.00	0.119
2	human (↓) + levee (↑)	2	0.37	204.26	1.83	0.048
3	arable (↑) + human (↓)	2	0.36	204.34	1.911	0.046
<b>Butterfly species richness</b>						
1	angle (↑) + length (↑) + mowing (↓) + shrub (↓)	4	0.62	147.35	0.00	0.032
2	angle (↑) + arable (↓) + length (↑) + mowing (↓) + shrub (↓)	5	0.65	148.22	0.97	0.020
3	angle (↑) + length (↑) + shrub (↓)	3	0.57	148.41	1.16	0.018
4	shrubs (↓) + wood (↑)	2	0.52	148.63	1.38	0.016
5	angle (↑) + human (↓) + shrub (↓)	3	0.56	148.67	1.42	0.016
6	angle (↑) + human (↓) + shrub (↓) + wood (↑)	4	0.60	148.99	1.74	0.013
7	human (↓) + shrub (↓)	2	0.51	149.03	1.78	0.013
8	shrubs (↓)	1	0.46	149.09	1.84	0.013
9	angle (↑) + human (↓) + shrub (↓)	3	0.56	149.15	1.90	0.012
<b>Butterfly abundance</b>						
1	length (↑) + mowing (↓) + shrub (↓)	3	0.46	237.00	0.00	0.039
2	human (↓) + mowing (↓) + shrub (↓)	3	0.46	237.19	0.19	0.035
3	mowing (↓) + shrub (↓)	2	0.39	237.83	0.82	0.026
4	mowing (↓) + native (↑)	3	0.44	238.13	1.12	0.022
5	angle (↑) + length (↑) + mowing (↓) + shrub (↓)	4	0.49	238.30	1.30	0.020
6	length (↑) + mowing (↓) + shrub (↓) + water (↓)	4	0.48	238.94	1.94	0.015

**Table 3**  
Estimates of the function slopes of variables present in the most parsimonious models characterizing plant and butterfly species richness and abundance by variables on river levees. Standard errors (SE) and 95% confidence limits (CL) are also presented. Name of variables as in Table 2.

Variable	Importance	Estimate	SE	Lower 95% LC	Upper 95% CL
<b>Plant species richness</b>					
human	0.961	-4.425	1.308	-6.988	-1.863
arable	0.277	1.326	0.383	0.576	2.076
levee	0.268	1.259	0.159	0.543	1.974
<b>Butterfly species richness</b>					
shrubs	0.996	-2.212	0.563	-3.317	-1.108
angle	0.557	0.960	0.300	0.373	1.548
length	0.438	1.008	0.293	0.433	1.583
wood	0.432	0.809	0.225	0.368	1.251
mowing	0.388	-0.745	0.202	-1.141	-0.348
human	0.360	-0.822	0.217	-1.248	-0.396
arable	0.279	-0.572	0.149	-0.846	-0.280
<b>Butterfly abundance</b>					
shrubs	0.801	-5.923	1.987	-9.818	-2.028
mowing	0.722	-4.911	1.652	-8.149	-1.674
human	0.425	-4.290	1.198	-6.639	-1.941
length	0.385	3.924	1.156	1.658	6.190
native	0.287	2.955	0.778	1.431	4.479
angle	0.278	2.561	0.690	1.209	3.914

plant species, suggesting that plants can use levees as dispersal pathways. The lack of patterns for butterflies indicates that these species do not use levees as dispersal routes. One of the possible explanations of why plant species used levees to disperse is that seed-disseminating animals move along linear habitats, especially across an urban landscape (Vittoz and Engler, 2007). Moreover, highly mobile species such as birds or mammals may transport seeds (epizo- and endo-zoochory) over great distances along linear habitats or edges (Vittoz and Engler, 2007). Similarly, winds which are commonly recorded along rivers, including urbanised areas (Wood et al., 2013), could propagate wind dispersed seeds. None of the species groups showed spatial patterns on control grasslands.

## 5. Conclusions

We showed that development of infrastructure such as levees along rivers may be beneficial to biodiversity in urban areas by the

creation of semi-natural habitats. Thus, possible positive impacts of human-mediated intervention in the landscape should be carefully identified and exploited for the conservation of plant-herbivore systems (Tryjanowski et al., 2013), especially in areas where there are no other options for nature conservation. Levees managed in such a manner as to prevent habitat degradation by substantial shrub cover would benefit open habitat species such as butterflies. Furthermore, mowing both slopes of a levee at different times might have a positive effect on pollinator conservation. Mowing should be performed after the flight season, in temperate weather and not earlier than the middle of September (Skórka et al., 2013). Shrubs are removed during regular maintenance, a positive side effect of which is that levees remain favourable habitats for many open-habitat species (Sýkora et al., 2009). Surprisingly, levee features such as angle and slope length did not affect most plant and butterfly species. Thus, the results show that levees of various sizes and shapes are possibly comparable for the sustainability of plant-

herbivore systems. Finally, the development of human settlements in close proximity to levees should be limited, in order to maintain high plant diversity. This would also reduce the negative economic impact of floods that regularly occur in the study area.

Although the mean number of invasive plant species on levees was marginally higher than on reference grasslands, there was no negative effect on native plants and butterflies. The absence of a negative impact appears to contradict earlier articles demonstrating that invasive plants have a significant, negative impact on pollinators (Moroń et al., 2009). However, invasive plants on levees rarely form dense mono-specific patches. When the density of the invasive species is low, it may benefit butterflies by adding a greater variety of foods accessible throughout the season, but if the density of invasive species increases, native plants become eliminated and as a result butterfly populations might decline (Moroń et al., 2009). The lack of impact of invasive species suggests no current need for the difficult and expensive elimination of invasive plants from levees. On the other hand, the invasive species that occur on levees may enter surrounding habitats (Hong et al., 2015) and have a more negative effect on plant-herbivore systems (Moroń et al., 2009).

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2017.04.052>.

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