Fragmentation of hardwood floodplain forests – how does it affect species composition?

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Abstract: The present study focuses on how spatial patch characteristics, such as patch area, shape and isolation, affect the natural species composition of hardwood floodplain forests. The natural species composition is defined according to species groups obtained using phytocoenological methods. The aim of the study was to establish the relationship between fragmentation indices and the number and proportion of species in each functional species group stated in this paper. This study is based on a dataset of 118 phytocoenological relevés sampled using the standard methodology of the Zürich-Montpellier School, ordered within the suballiance *Ulmenion* (mixed oak-elm-ash forests along the great rivers). The study area is situated in Central Europe, in the northern part of the Pannonian biogeographic region. The digital map of hardwood floodplain forests was rasterized to 25 m cell size. The FRAGSTATS software was used to obtain fragmentation indices, and generalised linear models tested the influence of forest patch fragmentation indices on species composition. Our analyses confirm that large hardwood floodplain forests are essential for natural species composition conservation, and that large fragment areas are highly susceptible to non-native species penetration. We also determined that small, compact fragments contain very valuable remnants of well-preserved natural hardwood floodplain forests with a high proportion of specialised *Ulmenion* species. However, disruption to hardwood floodplain forest natural borders engenders a greater threat to its natural species composition than decline in patch area, because disruption results in increased Shape index, increased contact with the surrounding environment, greater edge effect and a higher proportion of alien species in the forest community.

Abbreviation: ENN–Euclidean Nearest Neighbour.

Nomenclature: Marhold (1998) for taxa, Jarolímek et al. (2008) for syntaxa.

1. Introduction

Forest fragmentation is the division of a forest patch into smaller, isolated patches, with negative consequences for most native forest biota. Reasons for forest fragmentation are various, in the past mainly the need of agricultural land and pastures, recently building of new infrastructure, river regulations and construction of small dams. Fragmentation reduces total forest area, possibly resulting in some species' extinction (Murcia 1995). Fragmentation on the local scale is a dynamic process where habitats are progressively reduced to smaller patches which become more isolated and increasingly influenced by edge effects (Forman and Godron 1986, Franklin 2001, McGarigal et al. 2002, Reed et al. 1996). These spatial structure alterations produce community composition changes in remnant patches (Drinnan 2005, Echeverría et al. 2007, Laurance et al. 1998, Saunders et al. 1991). Fragments in anthropogenically altered forests are normally surrounded by a matrix of low biomass and structural complexity, such as pastures, croplands or young secondary forest stands (Murcia 1995).

As forest landscapes become increasingly fragmented, forest species populations are reduced, dispersal and migration patterns are interrupted, ecosystem inputs and outputs are altered and previously isolated core habitats become exposed to external conditions, these all result in a decline of natural biological diversity (Terborgh and Winter 1980, Tilman et al. 1994) or to the colonization of the area by light-demanding species from open habitats (Honnay et al. 2002).

Landscape factors such as the proportion of forest habitat in the landscape, the various sizes of fragments, the fragment shape and the degree of fragment isolation are the main factors reducing forest biodiversity. All these changes can increase fragment vulnerability to external influences, including shifts in plant species composition (Andrén 1994, Murcia 1995, Hill and Caswell 1999, Cooper and Walters 2002, Fahrig 2002, Laurance et al. 2002), biological invasions and decline in typical forest species populations. These changes tend to be more apparent in smaller fragments which are proportionately more affected by edge effect because of their higher edge/interior ratio, and because they support smaller

populations than larger fragments (Laurance and Yensen 1991, Goodman 1987).

Many consequences of forest fragmentation have prolonged lag effects and require sufficient "relaxation" period, with communities passing through a series of transitional states before final equilibrium is attained (Tilmanet al. 1994, Terborgh et al. 1997). Responses to isolation and habitat loss are therefore more significant in older fragments that have had adequate time to equilibrate (Turner et al. 1997). Long-lived species can remain in some environments for many years, even when conditions determining their occurrence undergo change (Inghe and Tamm 1985, Turner and Corlett 1996).

Studying the relationship between landscape patterns of forest fragments and species diversity is important for forest conservation and management purposes (Turner et al. 2001, Gutzwiller 2002), and forest reserve network planning frequently considers fragmentation patterns to preserve larger and less isolated forest fragments (Harris 1984, Ranta et al. 1998, Lambeck and Hobbs 2002). The inclusion of small fragments in protection networks is currently emphasized, because these small reserves can include high-quality remnants of endangered ecosystems, especially in chronically fragmented landscapes where large reserves include a higher proportion of degraded land (Schwartz 1999, Götmark and Thorell 2003). Among forest habitats, hardwood floodplain forests are most invaded by non-native species (Walter et al. 2005, Vilá et al. 2007, Pyšek et al. 2010), especially in the last few decades (Medvecká et al. 2013, Petrášová et al. 2013).

Hardwood floodplain forests featuring the great rivers' mixed oak, elm and ash forests are among the most fragmented forest habitats (Michalko 1987) which were widespread in the alluvia of lowland rivers from the neolithic era to the 12th century (Krippel 1986, Šomšák 1995). These became more and more fragmented after the 19th century, especially due to deforestation for the Danube Gabčíkovo dam (Generel 1976). Three large protected landscape areas and a number of smaller fragmented nature reserves were established to protect Slovak hardwood floodplain forests.

Our study focuses on how spatial patch characteristics, such as patch area, shape and isolation, affect the natural species composition of hardwood floodplain forests. In contrast to previous studies (e.g., Santos et al. 2007, Wu et al. 2013, Rösch 2015), the natural species composition is defined according to species groups obtained using phytocoenological methods. The aim of the study was to test the hypothesis that higher fragmentation influenced negatively the diversity of forest species groups and positively the occurrence of aliens.

2. Methods

2.1 Study area

The study area is situated in Central Europe, in the northern part of the Pannonian biogeographic region known as the central Danubian basin. The Carpathians encircle the region from the north. The main relief features are the dominant alluvial plains with sparse isolated low hills in the interior and low mountain ranges along the boundaries. The study area includes all Slovak lowland regions with large river alluvia. These exist in the Borská nížina Lowland along the Morava and Rudava rivers, in the Podunajská nížina Lowland along the Danube River and its Hron and Váh tributaries, and in the Východoslovenská nížina Lowland along the Topľa, Latorica and Bodrog rivers (Fig. 1).
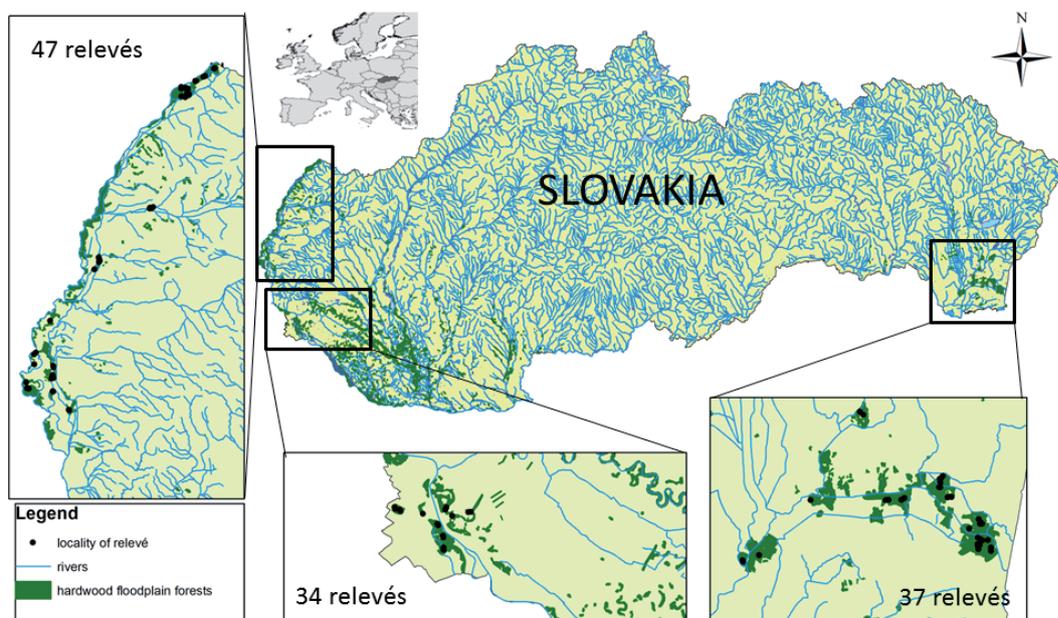
Figure 1. Map of the study area.

Table 1. List of species from each defined group. Species were identified according to the synoptic table of 2098 phytocoenological relevés from suballiance *Ulmenion* and adjacent syntaxa using the percentual frequency and fidelity concept (phi > 25).

Diagnostic species for *Ulmenion*	*Acer campestre, Allium ursinum, Brachypodium sylvaticum, Convallaria majalis, Crataegus ripidophylla. Fraxinus angustifolia, Populus alba, Quercus robur, Ulmus minor, Ulmus laevis*
Constant species for *Ulmenion*	*Alliaria petiolata, Arum alpinum, Campanula trachelium, Cornus sanguinea, Dactylis polygama, Euonymus europaeus, Galium aparine, Geranium robertianum, Glechoma hederacea, Moehringia trinervia, Polygonatum latifolium, Polygonatum multiflorum, Rubus caesius, Sambucus nigra, Stachys sylvatica, Viola mirabilis*
Diagnostic species for *Salicion albae*	*Alisma lanceolata, Caltha palustris, Calystegia sepium, Carex acutiformis, Carex riparia, Humulus lupulus, Galium palustre, Iris pseudacorus, Leucojum aestivum, Lysimachia vulgaris, Lythrum salicaria, Mentha aquatica, Poa palustris, Salix alba, Salix fragilis, Sium latifolium, Solanum dulcamara, Stachys palustris, Symphytum officinale*
Diagnostic species for *Carpinion betuli*	*Asarum europaeum, Astragalus glyciphyllos, Campanula rapunculoides, Carex digitata, Carex pilosa, Carpinus betulus, Clinopodium vulgare, Cruciata glabra, Dentaria bulbifera, Euphorbia amygdaloides, Fagus sylvatica, Galium odoratum, Galium schultesii, Glechoma hirsuta, Lathyrus niger, Lathyrus vernus, Luzula luzuloides, Melica uniflora, Mycelis muralis, Prunus avium, Quercus petraea, Symphytum tuberosum*
Archaeophytes	*Arctium lappa, Arctium minus, Ballota nigra, Chelidonium majus, Fallopia convolvulus, Juglans regia, Lamium purpureum, Parietaria officinalis, Viola odorata*
Neophytes	*Ailanthus altissima, Aster lanceolatus* agg., *Fraxinus pennsylvanica, Impatiens glandulifera, Impatiens parviflora, Juglans nigra, Negundo aceroides, Parthenocyssus quinquefolia, Robinia pseudoaccacia, Solidago canadensis, Solidago gigantea*

The hardwood floodplain forests are situated in higher positions on older river terraces with typical fluvisol and gleysol soils. They are affected by groundwater table fluctuations and, irregularly, by short-term flooding. In the tree layer, *Fraxinus angustifolia*, *Quercus robur*, *Ulmus minor* and *Ulmus laevis* dominate. The forests are classified within the class *Querco-Fagetea*, alliance *Alnion incanae*, suballiance *Ulmenion*. These forests covered a considerable part of the large Slovak lowlands in the neolithic era, before humans settled the territory (Krippel 1986, Michalko 1987). The Danube River formed large and dynamic branch systems until the end of the 12th century, until the need for river transport resulted in regulation of the branch system into one large river bed on the right side of the branch system. The decreased groundwater table in the remaining branch system encouraged agriculture in the regulated area. In addition, the vegetation cover changed considerably due to deforestation and fragmentation of the area (Generel 1976). An embankment system was constructed over an extended period to protect against flooding, and this was completed in the 19th century (Šomšák 1995). The embankments divided the river branch system into two parts, the first was closer to the main watercourse where flooding was more intensive and there the existing hardwood floodplain forests were transformed into willow-poplar forests or Canadian poplar plantations. The second part was outside the embankment where the groundwater table decreased and the hardwood floodplain forests degraded (Šomšák 1995). The main intervention in the floodplain forests during the last few decades has been the Gabčíkovo Dam construction, joining the Hrušovská zdrž Dam constructed between 1977 and 1991. The construction required clearing of 250 km2 of floodplain forest (Kozová et al. 1991), and the remnants of these forests are now amongst the most disturbed and altered ecosystems in Pannonia (Borhidi 1996).

2.2 Data collection

This study is based on a dataset of 118 phytocoenological relevés classified within the suballiance *Ulmenion* comprising riparian mixed oak-elm-ash forests along the great rivers. The localities were chosen using ArcGis 9.2 software according to the forestry map of recent hardwood floodplain forest distribution, and these cover all alluvial lowlands of the great Slovak rivers. Relevés were sampled in forest patches with different shapes and ranging in area from 650 m2 to 5,570 ha.They were made in internal forest environments, at least 20 meters from the forest edge, on plots where tree layers contain *Fraxinus angustifolia*, *Quercus robur*, *Ulmus laevis* or *U. minor* species, typical trees of hardwood floodplain forests. Relevés were sampled on 20 m × 20 m plot areas during the 2010 – 2012 vegetation seasons using the standard methodology of the Zürich-Montpellier school (Braun-Blanquet 1964, Westhoff and van der Maarel 1973). Species cover was recorded by the New Braun-Blanquet cover-abundance scale (Barkman et al. 1964). Relevés were stored in the TURBOVEG database (Hennekens and Schaminné 2001) and processed in the JUICE programme (Tichý 2002).

A large dataset of relevés from the Slovak national database of phytocoenological relevés (www.ibot.sav.sk/cdf) was used to identify specialised hardwood floodplain forest species groups. The selection of species in each group was based on phytocoenological principles. A synoptic table was

Table 2. Descriptive statistics of occurence of species from each functional group.

	Mean	Median	Min. - Max.	Variance	Std. Dev.
Total number of species	31.65	33	9 - 48	51.80	7.20
Ulmenion diagnostic species	9.86	10	5 - 15	7.23	2.69
Ulmenion constant species	16.84	17	2 - 28	29.74	5.45
Salicion diagnostic species	0.80	0	0 - 7	2.15	1.47
Carpinion diagnostic species	1.68	1	0 - 6	2.32	1.52
Archeophytes	0.31	0	0 - 3	0.35	0.59
Neophytes	1.59	1	0 - 11	4.17	2.04

compiled from the dataset of relevés assigned to the suballiance *Ulmenion* and from the following alliances adjacent to hardwood floodplain forests in the landscape – *Salicion albae* and *Carpinion betuli*, 506 relevés were classified within *Ulmenion*, 264 relevés within *Salicion albae* and 1328 relevés within *Carpinion betuli*. Diagnostic species of *Salicion albae* and *Carpinion betuli* (according to "Diagnostic, constant and dominant species of higher vegetation units of Slovakia" (Jarolímek et al. 2008)) and percentage frequency and fidelity concept (phi>25) were employed to identify diagnostic and constant species of the *Ulmenion* suballiance, they represent "typical forest species". Fisher's test (p<0.005) eliminated species with non-significant occurrence (Chytrý et al. 2002, Chytrý et al. 2007). "Alien species", archaeophytes and neophytes were assigned according to the Slovak list of non-native species (Medvecká et al. 2012). The species groups are presented in Table 1.

2.3 Statistical analysis

The digital map of hardwood floodplain forests was rasterized to 25 m cell grid size. FRAGSTATS software was used to obtain the following fragmentation indices: patch area, patch perimeter, Shape index, Contiguity index and isolation via Euclidean nearest neighbour distance (ENN).

Shape index: Patton's (1975) Shape index measures the complexity of patch shape compared to a circle of the same size, and is therefore independent of patch area. This shape index is widely applied in landscape ecological research (Forman and Godron 1986). The Shape index attains 1 when the patch is circular, and it increases without limit as the patch shape becomes more irregular.

Contiguity index: A further method of assessing patch shape is based on the spatial connectedness, or contiguity, of cells in a grid-cell patch. This provides an index on patch boundary configuration, and thus patch shape (LaGro 1991). This index is 0 for a one-pixel patch and increases to a limit of 1 as patch contiguity, or connectedness, increases.

Isolation: Patch isolation plays a critical role in both island biogeographic theory (MacArthur and Wilson 1967) and metapopulation theory (Levins 1970, Gilpin and Hanski 1991). Euclidean nearest neighbour distance (ENN) is a simple measure of patch isolation, where EEN is defined in Euclidean geometry as the length of the shortest straight-line between the focal patch and its nearest neighbour of the same class. It is based on the distance between the cell centres of the two closest cells in respective patches (McGarigal 2002).

Generalised linear models (GLM) tested the influence of forest patch fragmentation indices on the number of species from defined species groups and proportion of species from each functional group. The influence on the number of species from each species group was determined by GLM with Poisson distribution family and log-link function, and GLM with binomial distribution family weighted by species number and log-link function tested the influence on the proportional representation of species groups. Several models were created by excluding non-significant variables, and resultant models were chosen by minimizing AIC criteria. The final models contain at least two significant factors, the graphs for each factor were made by fitting other relevant variables to their mean value. GLM was carried out by the ade4 package (Chessel et al. 2013) using R-software (R Development Core Team 2012)

3. Results

3.1 Number of species

Among European forest habitats, hardwood floodplain forests are one of the species richest forest ecosystems, although the number of species is very variable. In relevés we analysed it varies from 9 to 48 species per relevé. The level of invasion varies from relevés without neophytes to the most invaded forests with 11 neophytes presented in a relevé. Statistical measures of species from each group are summarized in Table 2.

The largest patches contain the highest total number of species (Fig. 2) and a higher number of *Ulmenion* diagnostic and constant species than smaller patches (Fig. 3). Isolation negatively affects the number of *Ulmenion* species (Fig. 4), where *Ulmenion* species number is lower in more isolated than in less isolated patches (Table 3). Although the number of neophytes bears no significant relationship to patch area, the patch perimeter affects it negatively because smaller perimeters indicate relatively smaller patches. The forest patch Shape index, however, affects number of neophyte, where increased shape index indicates more complicated patch shapes,

Table 3. Fragmentation indices affecting the number of species from each species group with their significance calculated using Generalised Linear Model. Minimal adequate model was fitted with a Poisson family and log link function. Standardized estimates, their standard errors and significance are presented.

	Estimate	Standard Error	P-value
Number of species (residual deviance=167.04 and d.f.= 113)			
(Intercept)	2.9370	0.0839	< 0.0001
Area	0.0005	0.0001	< 0.0001
Perimeter	-0.0001	< 0.0001	< 0.0001
Shape Index	0.3112	0.0533	< 0.0001
Number of *Ulmenion* diagnostic and constant species (residual deviance=185.28 and d.f.= 114)			
(Intercept)	3.2650	0.0280	< 0.0001
Area	0.0001	< 0.0001	0.0098
Isolation (ENN)	-0.0001	< 0.0001	0.0131
Number of neophytes (residual deviance=235.05 and d.f.= 113)			
(Intercept)	-0.9480	0.1144	0.0201
Area	0.0004	0.0006	0.3900
Perimeter	-0.0001	< 0.0001	0.0091
Shape Index	0.9077	0.2184	< 0.0001
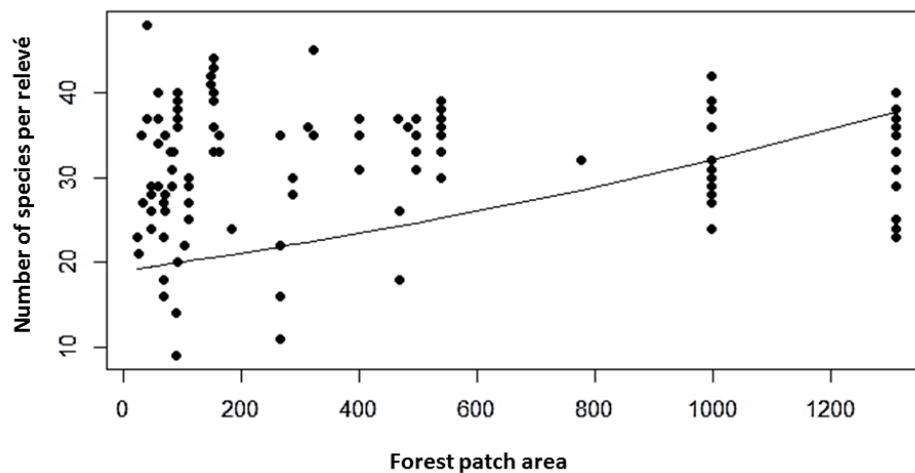
Figure 2. Relationship between the number of species in the relevé and forest patch area (ha). The prediction line was calculated by GLM with Poisson distribution family and log-link function (with intercept 2.937, standardised estimates 0.0005 and significance 0.0001).

irregular boundaries and greater contact with the surrounding environment. These patches accumulate a higher number of neophytes (Fig. 5). In addition, the number of *Carpinion* and *Salicion* species and archaeophytes is not significantly affected by analysed fragmentation indices.

3.2 Species proportions

The proportion of species groups is more precisely explained by fragmentation indices than by species number. Models with significant variables were created to determine the proportion of *Ulmenion* diagnostic species, *Ulmenion* constant species, Neophytes and all alien species together (neophytes and archaeophytes) (Table 4).

The neophyte proportion was unaffected by patch area, the proportion of all alien species (neophytes together with archaeophytes) is higher in larger patches and the patch perimeter negatively affects the proportion of neophytes and all alien species.

The effect of patch area on the proportion of *Ulmenion* species is not explicit. The proportion of highly specialised *Ulmenion* diagnostic species was higher in smaller patches and the proportion of *Ulmenion* constant species increased in larger patches (Table 4).

Decreased shape index indicates compact patch shape with continuous natural boundaries, and a larger proportion of *Ulmenion* species is present in these patches compared to patches with high shape index (Fig. 6). In contrast, increased

shape and contiguity index indicate more complicated patch shape, irregular boundaries and higher contact with the surrounding environment. The proportion of *Ulmenion* species is lower in these patches and the neophyte proportion is higher (Fig. 7).

Discussion

Total number of species

Many studies have concentrated on explaining how forest ecosystem fragmentation affects forest species diversity, the composition of species with different life strategies and species from different functional groups. Some have suggested that the effect of habitat fragmentation on plant diversity is linearly negative (Laurance et al. 2001), positive (Dolt et al. 2005) or non-linearly negative (Digiovinazzo et al. 2010).

Our results demonstrated that total number of species is positively related to increasing forest fragment area. While this relationship is a fundamental and long-accepted aspect of community ecology (Watson 1983, Connor and McCoy 1979, Gilbert 1980), more recent studies present different findings. For example, Santos (2007) from a Brazilian forest reported that most variation in forest fragment species composition was unrelated to fragment area.

No relationship between plant species richness and fragment size was found in grasslands (Rösch et al. 2015). A time lag exists in plant communities' response to changes in habi-
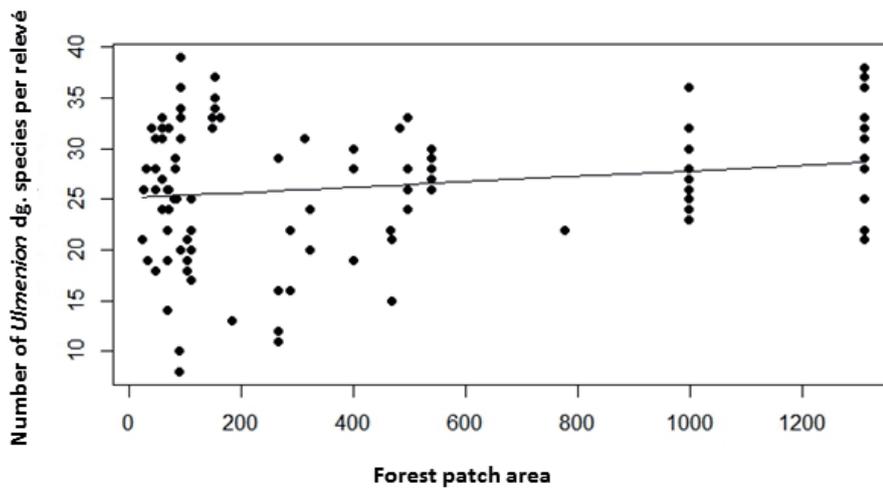
Figure 3. Relationship between number of *Ulmenion* diagnostic and constant species in the relevé and forest patch area (ha). The prediction line was calculated by GLM with Poisson distribution family and log-link function (with intercept 3.265, standardised estimates 0.001 and significance 0.0098).
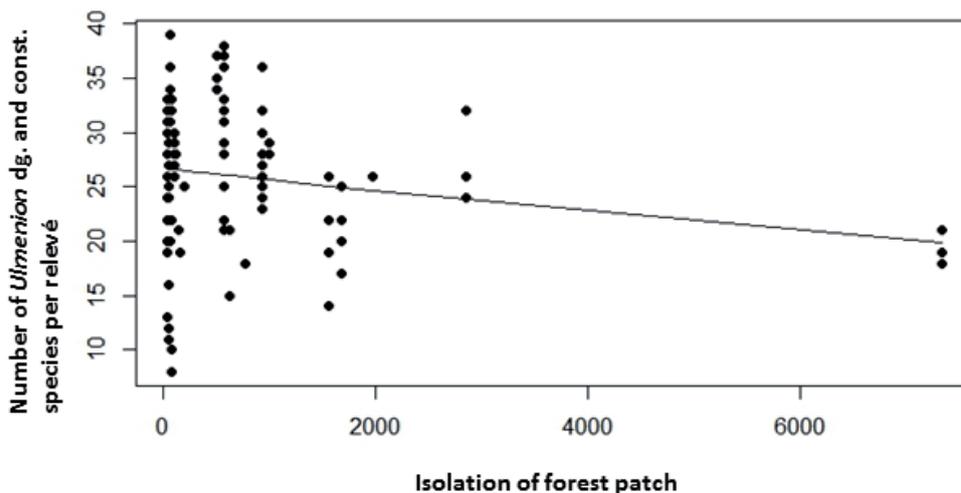
Figure 4. Relationship between number of *Ulmenion* diagnostic and constant species in the relevé and forest patch isolation (m). The prediction line was calculated by GLM,with Poisson distribution family and log-link function (with intercept 3.265, standardised estimates -0.001 and significance 0.0131).

Table 4. Fragmentation indices affecting the proportion of species from each group with their significance calculated using Generalised Linear Model. Minimal adequate model was fitted with a binomial distribution family and log link function. Standardized estimates, their standard errors and significance are presented.

	Estimate	Standard Error	P-value
Proportion of *Ulmenion* diagnostic species (residual deviance=124.53 and d.f.= 112)			
(Intercept)	6.4280	3.2520	0.0481
Area	-0.0011	0.0003	0.0001
Perimeter	0.0001	< 0.0001	0.0001
Shape Index	-0.7016	0.1846	0.0002
Contiguity Index	-6.6180	3.2430	0.0413
Proportion of *Ulmenion* constant species (residual deviance=140.01 and d.f.= 113)			
(Intercept)	5.7109	2.0481	0.0053
Area	0.0006	0.0001	< 0.0001
Shape Index	-0.2850	0.0449	< 0.0001
Contiguity Index	-5.3692	0.0010	0.0122
Proportion of neophytes (residual deviance=267.47 and d.f.= 112)			
(Intercept)	-29.1200	7.1220	0.0005
Area	0.0010	0.0007	0.1562
Perimeter	-0.0001	0.0000	0.0004
Shape Index	1.8080	0.3949	< 0.0001
Contiguity Index	25.0400	7.0940	0.0004
Proportion of aliens - neophytes+archaeophytes (residual deviance=371.1 and d.f.= 112)			
(Intercept)	-22.2400	5.4500	< 0.0001
Area	0.0012	< 0.0001	0.0343
Perimeter	-0.0001	< 0.0001	< 0.0001
Shape Index	1.5400	0.3128	< 0.0001
Contiguity Index	18.9000	5.4170	0.0004
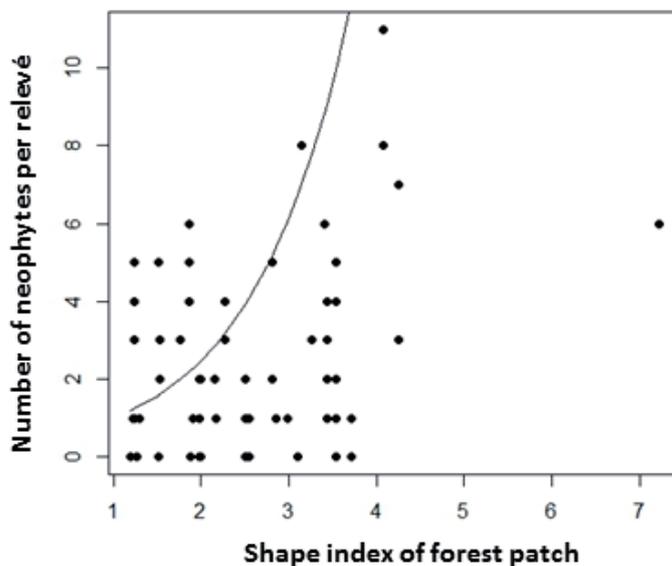
Figure 5. Relationship between the number of neophytes in the relevé and forest patch Shape index. The prediction line was calculated by GLM with Poisson distribution family and log-link function (with intercept -0.948, standardised estimates 0.9077 and significance 0.0001).

tat configuration, as demonstrated by Lindborg and Eriksson (2004), and this may also contribute to the inconsistent species-area effects observed in Santos et al.'s (2007) fragments. It appears that larger fragments house more species than same area plots in continuous habitats because these fragments collectively have a larger boundary. This enables higher penetration of exotic species, and species number reaches saturation when a fragment is large enough (Wu et al. 2013). These frag-

ments achieve higher total diversity from increasing ruderal and non-native species diversity, rather than from natural diversity effects so it is not a sign of good condition of habitat.

Typical forest species occurrence

The actual effects of fragmentation are better understandable by dividing the species dataset into species groups. A fine
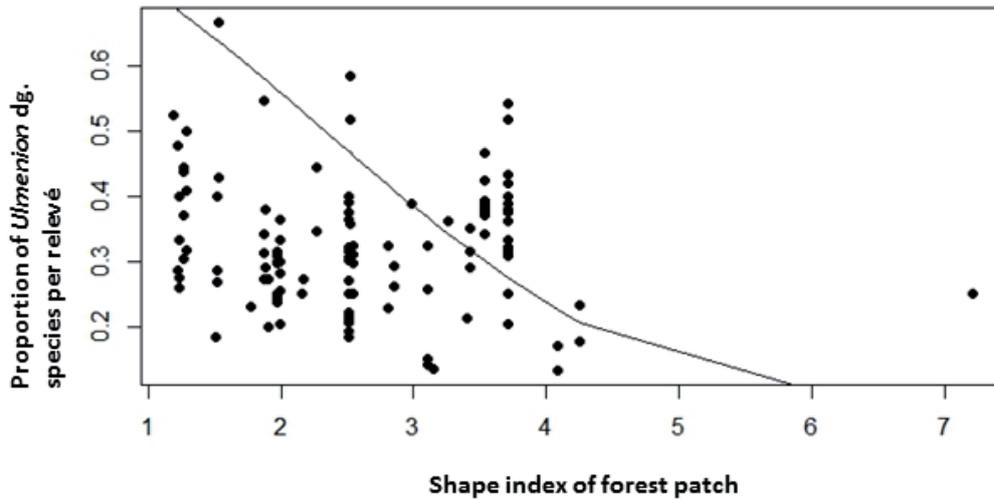
Figure 6. Relationship between the proportion of *Ulmenion* diagnostic species and forest patch Shape index. The prediction line was calculated by GLM with binomial distribution family weighted by species number and log-link function (with intercept 6.428, standardised estimates -7.016 and significance 0.0002).

Figure 7. Relationship between the proportion of neophytes and forest patch Contiguity index. The prediction line was calculated by GLM with binomial distribution family weighted by species number and log-link function (with intercept -29.12, standardised estimates 25.04 and significance 0.004).
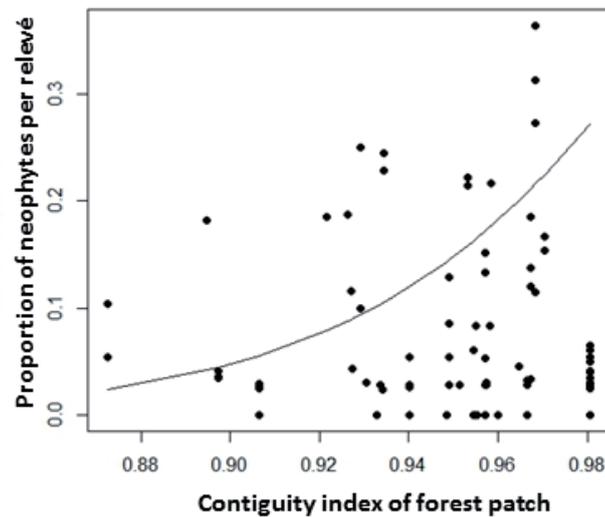
detailed scale was used to identify hardwood floodplain forest specialists in our study by phytocoenological methods. An important finding in our study is that the number of "typical forest species" (*Ulmenion* diagnostic and constant species) increases in larger and less isolated fragments. Connectivity of fragments was the most significant factor influencing the number of typical semi-dry grasslands and Red List species in semi-dry hay meadows of Alpine Foreland of Styria (Sengl et al. 2016).

We found occasional shift from positive to negative relationship between habitat fragmentation and species richness with intensified fragmentation, while Wu et al. (2013) reported that the number of plant functional groups increased due to habitat fragmentation, and different functional groups exhibited distinct response to the degree of fragmentation.

Our results highlighted negative fragmentation effect on *Ulmenion* diagnostic and constant species, and that the im-

pact of fragmentation on forest species of adjacent communities *Salicion albae* and *Carpinion betuli* was statistically non-significant. This fact may occur because these species form an admixture in *Ulmenion* forests with low cover, and their occurrence is less dependent on the hardwood floodplain forest interior environment. Similar results, with a more generalized definition of species groups, were published in Hill and Curran's (2001) tropical rainforest research which reported that large forest fragments contain the greatest number of tree species. The relative proportions of evergreen and shade-tolerating species increase over deciduous pioneers as forest fragment area increases, due to size-related core area/edge effects where the interior area increases more than the forest edge zone (Hill 2001). Tabarelli et al. (1999) concurred that forest fragment area is a major determinant of woody species guilds in old montane Atlantic forests.

Aliens occurence

Processes caused by fragmentation, especially invasion by non-native species, are considered a major threat to natural forest original ecosystem diversity (Williamson 1996, Kowarik 2003, Weber 2003, Kettunen et al. 2009, Pyšek et al. 2010). Kapos (1989), Laurance (1990) and Malcolm (1994) concur that the establishment of ruderal (sensu Sudnik-Wojcikovska and Kozniewska) and neophyte species is clearly related to structural and microclimatic changes in fragmented forests. Although our study revealed a non-significant relationship between fragment area and the number of neophytes and archaeophytes, smaller perimeters, denoting smaller patches, affected the number of neophytes positively.

Species' proportions are also appropriate indicators for assessing ecosystem conditions. Larger fragments concentrate a higher proportion of *Ulmenion* constant species well-adapted to hardwood floodplain forest conditions. Although neophytes (sensu Richardson et al. 2000, Pyšek et al. 2004) are reportedly unaffected by fragment area, the combined proportion of all aliens, including archaeophytes, is higher in large fragments. Results of other studies do not clearly indicate negative or positive effects of fragmentation on alien species' richness.

Tabarelli et al. (1999) report that key flora components in small old montane Atlantic forest fragments less than 10 ha in area cannot be distinguished from those in edge habitats. With increasing number of alien species, the species composition tended to converge in small forest fragments which preserved only a limited and changed subset of original plant community species (Patterson 1987). Tabarelli et al. (1999) added that alien species were considerably more prevalent in small fragments of Atlantic rainfall forests, and that their species richness was negatively correlated with fragment size.

Shape of forest patch

Since the effect of fragment area on the number or proportion of alien species was not explicit in our results, the effect of alternate fragmentation indices appears more important, highlighting our confirmation that Shape index is the most important factor affecting species functional group proportions. Increased shape index indicates more complicated patch shape, irregular boundaries by gaps created by anthropogenic clear-cuts, together with decreased total interior habitat and increased boundary contact with the surrounding environment. Higher solar radiation levels in open adjacent habitats outside the fragments increases air temperature, wind speed, and light availability, resulting in lower air and soil humidity at the fragment edges (Zuidema et al. 1996). In addition, disturbance-adapted alien species slowly modify natural forest floristic and guild composition by dispersing in gaps created by natural tree-fall in forest edges (Janzen 1986). Hence, the proportion of *Ulmenion* species is lower and neophytes higher in these patches with elevated Shape index.

Variations in total species composition are explained by a combination of fragment area and disturbance intensity, rather than solely by fragment area (Honnay et al. 1999, Ross et al. 2002). These authors determined that disturbance was the major factor interacting with area in influencing fragment species richness and composition. This interaction is due to increased disturbance sensitivity as fragments become smaller, and it is also related to the increased Shape index and concurred that anthropogenic disturbance promotes alien species invasion in forest patches (Fox 1986, Hobbs 1988).

Conclusion

Although complete habitat loss is recognized as the most important factor responsible for biodiversity decline in wildlife communities, habitat fragmentation has a subordinate role (Fahrig 2002, 2003). Fragmentation has less, but more variable, effects dependent on individual forest ecosystems and species functional groups (Trzcinski et al. 1999).

Our analyses confirm that large hardwood floodplain forests are essential for natural species composition conservation, and that large fragment areas are highly susceptible to non-native species penetration. We also determined that small compact fragments contain very valuable remnants of well preserved natural hardwood floodplain forests with a high proportion of specialised *Ulmenion* species. Disruption of hardwood floodplain forest natural borders engenders a greater threat to its natural species composition than decline in patch area and results in increased Shape index, increased contact with the surrounding environment, greater edge effect and a higher proportion of non-native species in the forest community.

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