

APTARA	INS	ins12504	Dispatch: July 10, 2017	CE: AFL
	Journal	MSP No.	No. of pages: 10	PE: Rod

*Insect Science* (2017) 00, 1–10, DOI 10.1111/1744-7917.12504

## ORIGINAL ARTICLE

# Environmental filtering is the main assembly rule of ground beetles in the forest and its edge but not in the adjacent grassland

Tibor Magura<sup>1</sup>  and Gábor L. Lövei<sup>2</sup>

<sup>1</sup>Department of Ecology, University of Debrecen, Debrecen, Hungary and <sup>2</sup>Department of Agroecology, Flakkebjerg Research Centre, Aarhus University, Slagelse, Denmark

**Abstract** In a fragmented landscape, transitional zones between neighboring habitats are common, and our understanding of community organizational forces across such habitats is important. Edge studies are numerous, but the majority of them utilize information on species richness and abundance. Abundance and taxonomic diversity, however, provide little information on the functioning and phylogeny of the co-existing species. Combining the evaluation of their functional and phylogenetic relationships, we aimed to assess whether ground beetle assemblages are deterministically or stochastically structured along grassland–forest gradients. Our results showed different community assembly rules on opposite sides of the forest edge. In the grassland, co-occurring species were functionally and phylogenetically not different from the random null model, indicating a random assembly process. Contrary to this, at the forest edge and the interior, co-occurring species showed functional and phylogenetic clustering, thus environmental filtering was the likely process structuring carabid assemblages. Community assembly in the grassland was considerably affected by asymmetrical species flows (spillover) across the forest edge: more forest species penetrated into the grassland than open-habitat and generalist species entered into the forest. This asymmetrical species flow underlines the importance of the filter function of forest edges. As unfavorable, human-induced changes to the structure, composition and characteristics of forest edges may alter their filter function, edges have to be specifically considered during conservation management.

**Key words** asymmetrical species flow; coexisting species; functional features; phylogeny; random process; traits

## Introduction

Habitat edges (also termed ecotones, boundaries, borders, or interfaces) are transitional zones between neighboring habitats (Forman & Godron, 1986; Turner *et al.*, 2001), and have an important role in controlling flows of organisms and materials across adjacent ecological elements (Cadenasso *et al.*, 2003; Ries & Sisk, 2004) and are fre-

quent subjects of study from both theoretical and practical points of view. Edges forming transition zones between forest interiors and adjacent open habitats (e.g., croplands, meadows, grasslands, clear-cuttings or regenerating plantations with open canopy) are common and increasing within terrestrial landscapes (Murcia, 1995): 20% of the world's remaining forests have an edge within 100 m, and 70% within 1 km (Haddad *et al.*, 2015). Solar radiation, light intensity, air and soil temperature, air and soil humidity, and wind intensity are altered at the forest edges, compared to either of the 2 neighboring habitats (Kapos, 1989; Matlack, 1994; Murcia, 1995). The consequences

Correspondence: Tibor Magura, Department of Ecology, University of Debrecen, Egyetem sq. 1, H-4032 Debrecen, Hungary. Email: maguratibor@gmail.com

are changes in tree and seedling density, canopy grasses, herbs and understory cover, seedling and plant growth, canopy damage and mortality (Murcia, 1995; Ries *et al.*, 2004; Laurance *et al.*, 2006). These changes, separately or in concert are likely to influence community assembly processes as well (Debastiani *et al.*, 2015).

Previous studies addressing the effects of changes in environmental, compositional and structural parameters at forest edges (the “edge effect”; Murcia, 1995) have usually evaluated the abundance and/or taxonomic diversity (species richness and/or species diversity; for mammals Schlinkert *et al.*, 2016; for birds Terraube *et al.*, 2016; for amphibians and reptiles Schneider-Maunoury *et al.*, 2016; for invertebrates Lövei *et al.*, 2006; Tóthmérész *et al.*, 2014; Bogyó *et al.*, 2015; Yekwayo *et al.*, 2016). Abundance and taxonomic diversity, however, contain little information on the mechanisms influencing patterns of community assembly, although such information is essential in biodiversity research (Swenson, 2013).

Differences (or similarities) in species characteristics are key variables in evaluating community assembly, because assembly mechanisms act on the similarities and differences of the constituting organisms (Cadotte *et al.*, 2013). Functional and phylogenetic information can be used to quantify such differences, because functionally similar species are likely to utilize the same resources, while phylogenetically related species may share many morphological and ecological traits through their common origin and evolutionary history (Webb *et al.*, 2002). Therefore, incorporating the functional and phylogenetic relatedness of community-forming species may enhance our understanding of the studied community (Cadotte *et al.*, 2010; Swenson, 2013; Magura, 2017). Several recent edge-related studies sought such understanding using functional (Ma & Herzon, 2014; Barbaro *et al.*, 2014), phylogenetic (Dodonov *et al.*, 2014; Peralta *et al.*, 2015), or combined (Luza *et al.*, 2015) approaches.

Ecological communities at local scales are assembled from regional species pools according to various assembly rules, which can be deterministic (habitat/environmental filtering, ecological interactions) or random processes (Pausas & Verdú, 2010). Various environmental factors may act as filters: species with appropriate traits and tolerance limits can persist (Magura *et al.*, 2015), while species that lack those traits (Keddy, 1992) or tolerance limits are filtered out. Environmental filters operating on conserved traits cause functional and phylogenetic clustering (underdispersion), and under this scenario, co-occurring species will be functionally and phylogenetically more similar than predicted by chance (Webb *et al.*, 2002; Pausas & Verdú, 2010). Environmental filtering operat-

ing on convergent traits, on the other hand, generate functional clustering, but phylogenetic repulsion (overdispersion), since the co-occurring species will be functionally more, but phylogenetically less similar than predicted by chance (Webb *et al.*, 2002). Species interactions (e.g., competition, facilitation) acting on conserved traits cause functional as well as phylogenetic repulsion: closely related species with similar traits will be excluded, and co-existing species will become functionally and phylogenetically less similar than predicted by chance (Webb *et al.*, 2002). If random processes govern the community assembly process, these, being independent of the functional or phylogenetic relatedness of species, will cause a situation where co-occurring species will be functionally or/and phylogenetically not different from randomly generated “null” assemblages (Webb *et al.*, 2002; Hubbell, 2006).

Although understanding the rules determining community assembly patterns from regional pools represents a fundamental topic in ecology and conservation biology (Vellend, 2010), the mechanisms and underlying patterns of community assembly along grassland–forest gradients are rarely studied. Species co-occurrence patterns of lichens (Belinchón *et al.*, 2012), woody plants (Debastiani *et al.*, 2015) and small mammals (Luza *et al.*, 2015) along grassland–forest gradients were examined, but similar analyses on invertebrates seem to be missing. Our study aimed to evaluate the assembly processes underlying the coexistence of ground beetles (Coleoptera: Carabidae) across an edge gradient between natural grassland and native forest in Hungary. Ground beetles are highly suitable subjects for such a study, because they are taxonomically well known, common in most terrestrial habitats, can easily be collected using standard methods (Lövei & Sunderland, 1996; Gerlach *et al.*, 2013), and several congeners frequently co-occur, making them an appropriate group to explore community assembly mechanisms. Several studies have evaluated spatial distribution and coexistence patterns of ground beetles along grassland–forest gradients (Magura *et al.*, 2000; Magura, 2002; Taboada *et al.*, 2004; Máthé, 2006; Elek & Tóthmérész, 2011), but none of these included functional and phylogenetic aspects (but see Magura, 2017). Using functional and phylogenetic similarities among species, we aimed to assess whether ground beetle assemblages are deterministically or stochastically structured across the edge. Our first hypothesis (H1) was that the specific sets of environmental conditions in both grasslands and in forest interiors would impose strong environmental filtering, and select related species with specific traits that allow to cope with these specific habitat conditions. Consequently, co-occurring species in either of these 2 habitats would be functionally

and phylogenetically more similar than predicted by chance (functional and phylogenetic clustering). Conversely, we expected (H2) low similarity between species due to effective niche partitioning in natural forest edges with diverse and abundant resources and microhabitats (Cadenasso *et al.*, 2003; Harper *et al.*, 2005). This effective niche partitioning could cause functional and phylogenetic repulsion, when co-existing species are functionally and phylogenetically less similar than predicted by chance.

## Materials and methods

### Study area and sampling methods

The study was conducted in a natural patchwork of forest-grassland in the Aggtelek karst region, in the northern Hungarian mountains (48°31'N, 20°31'E). The studied native stands were 60-year-old oak-hornbeam forests (*Quercus-Carpinetum*) with closed canopies, a thick leaf litter layer (4–6 cm of depth), and moderately dense herbaceous and shrub layers (cover of 20%–30%). This forest association is the most extensive in this region, and can be considered the “matrix.” Natural, moderately dry grassland patches (*Polygalo majori-Brachypodium pinnati*) were embedded within this forest matrix. Exposure will influence abiotic conditions (sunshine, wind effects, relative humidity), and thus we always selected east-facing edges and their adjoining grassland patches. The study sites were in a protected area, neither disturbed nor under forestry management during the last 50 years.

Three sites, located at 150–200 m from each other were selected for study. At each site, 6 lines of 7 pitfall traps each were operated during the snow-free period (March–October). Individual traps were 2 m from each other. Two such lines (10 m from each other to ensure spatial independence, see Digweed *et al.*, 1995) were deployed in the grassland, at the edge and in the forest interior. The grassland and forest lines were min. 50 m from the respective edges; the edge trap lines were set 5 m from the grassland border, and the other one 5 m from the forest one. Traps consisted of 100 mm diameter plastic cups (volume 500 mL) and contained about 200 mL 70% ethylene glycol as a killing-preserving solution and a drop of detergent to break the surface tension. Pitfall traps were protected by a fiberboard from litter and rain. Samples were collected monthly, and catches were pooled by trap line over the whole sampling period, resulting in 18 data sets (3 sites × 6 trap lines each). Beetles caught were identified to species using standard keys (Hürka, 1996).

### Data analyses on functional and phylogenetic features

The analysis of functional features of species used both life-history traits (related to morphology, reproduction, dispersal and resource use) and ecological traits. The following life-history traits were included:

**body size:** characterized by the geometric mean of the elytral length range, in mm,

**wing morphology:** brachypterous, dimorphic, macropterous,

**mode of overwintering:** larval versus adult,

**activity:** day- or night-active, and

**feeding:** herbivorous, mixed feeder, or predator.

The ecological traits evaluated included habitat affinity (forest specialist, grassland specialist, habitat generalist) and humidity preference (hygrophilous, mesophilous, xerophilous). All the above traits were selected *a priori* (Spake *et al.*, 2016) and collected from the literature (Koch, 1989; Laroche, 1990; Hürka, 1996; Gerisch, 2014).

Distances between species based on functional traits (FDist) were calculated using Gower's distance metric (Gower, 1971), computed using the *StatMatch* package (D'Orazio *et al.*, 2006). Body size was regarded as continuous (numerical), while the other traits as categorical (nominal) variables. FDist values ranged from 0 to 1. Phylogenetic (evolutionary) distance (PDist) among ground beetle species was characterized by the distance between species based on the branch length to the common ancestor on Beutel *et al.*'s (2008) phylogenetic tree. The branch length of a phylogenetic tree is a commonly used distance measure to express phylogenetic relatedness (e.g., Heikkala *et al.*, 2016). Distances between species based on the branch length to the common ancestor were converted to values ranged from 0 to 1 (with the highest value made equal to 1, and the others recalculated proportionally to this), to set FDist and PDist on the same scale.

The evolution of the studied functional traits (conservatism and convergence) was assessed by studying the relationship between functional and phylogenetic distances (phylogenetic signal). To evaluate whether the studied functional traits have been conserved over time, the correlation between the functional distance matrix and the phylogenetic distance matrix was analyzed by a Mantel test using the *ade4* package with 9 999 replications (Dray & Dufour, 2007).

Functional and phylogenetic features may provide complementary information about species differences. To integrate information measuring species differences, Cadotte *et al.* (2013) proposed that the distances between species in the trait-space and the distances between

species in the phylogenetic-space should be combined as functional–phylogenetic distance (FPDist):

$$FPDist = (a PDist^p + (1 - a) FDist^p)^{1/p},$$

where  $PDist$  is the phylogenetic distance;  $FDist$  is the functional distance,  $p$  is an integer to ensure nonlinearity, while  $a$  is the weighting parameter, which determines the contribution of  $PDist$  and  $FDist$  to  $FPDist$ . When  $a = 1$ ,  $FPDist$  only includes phylogenetic distance and when  $a = 0$ ,  $FPDist$  only includes functional distance. The advantage of this integrative approach is that during the consideration of similarity among species beside the selected traits, unmeasured, but phylogenetically correlated traits are also considered, since phylogeny may provide additional or even complementary information to functional traits (Cadotte *et al.*, 2013). During the calculations we used  $p = 2$ , as recommended by Cadotte *et al.* (2013).

We first calculated the mean pairwise functional–phylogenetic distance (MFPD) for 41 levels of the functional–phylogenetic weighting parameter ( $a$ ) from 0 to 1 by increasing  $a$  in steps of 0.025. Second, for all 41 levels of the weighting parameter ( $a$ ), to gain independence from the number of species per sample, we calculated the standardized effect sizes (SES) using the observed MFPD of the species collected in each trap line ( $MFPD_{\text{observed}}$ ) and the same of an equal number of randomly selected species from the regional species pool (all species recorded in this study;  $MFPD_{\text{random}}$ ). Standardized effect sizes were calculated as

$$SES = (MFPD_{\text{observed}} - MFPD_{\text{random}}) / SD_{MFPD_{\text{random}}},$$

where  $SD_{MFPD_{\text{random}}}$  is the standard deviation of  $MFPD_{\text{random}}$ . Creating an appropriate random model using species recorded in the study sites is a standard method to test assembly rules (Cadotte *et al.*, 2013; Heikkala *et al.*, 2016). The standardized effect sizes were calculated based on null models with 999 randomizations by tip shuffling (Webb *et al.*, 2002) using the *picante* package (Kembel *et al.*, 2010). Third, we defined the optimal value of the weighting parameter ( $a$ ), where pattern explanation is maximized. The strength of the relationship between the standardized effect sizes and position along the grassland–forest gradient was tested by systematically changing the phylogenetic-weighting parameter ( $a$ ) using linear models with the function *lm*. The optimal value of the weighting parameter ( $a$ ) was the one under which the adjusted  $R^2$  value of the linear model between the standardized effect sizes and position along the grassland–forest gradient reached its maximum (Cadotte *et al.*, 2013; Bässler *et al.*, 2016; Heikkala *et al.*, 2016). Finally, we evaluated

the mean standardized effect sizes calculated for the optimal value of the weighting parameter ( $a$ ). If communities are stochastically structured, the mean standardized effect sizes are equal to zero (Webb *et al.*, 2002). Nonzero values of the standardized effect sizes indicate deterministic processes. Negative values indicate functional and phylogenetic clustering, which is a sign of environmental filtering, while positive values indicate repulsion, resulting from species interactions (Webb *et al.*, 2002; Pausas & Verdú, 2010). Confidence intervals of the standardized effect sizes were calculated using the *boot* package with 999 iterations (Davison & Hinkley, 1997). All analyses were conducted in the R program environment, version 3.3.2 (R Core Team, 2014).

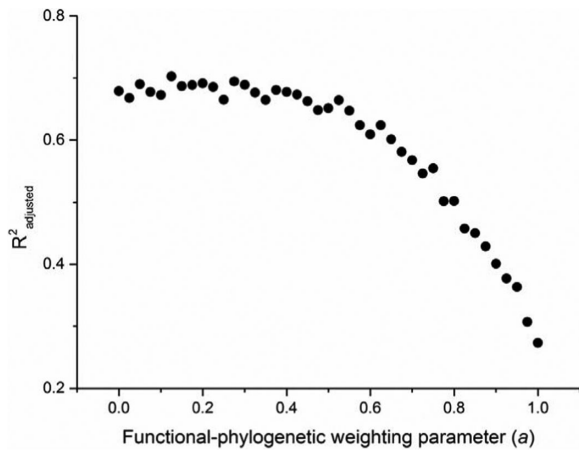
## Results

A sampling effort of 32 760 trap-days (126 traps  $\times$  260 d) collected 4 339 individuals of 40 ground beetle species. This included 37 species with 862 individuals in the grassland, 1 267 individuals of 23 species at the forest edge, and 18 species with 2 210 individuals in the forest interior (see Magura, 2017).

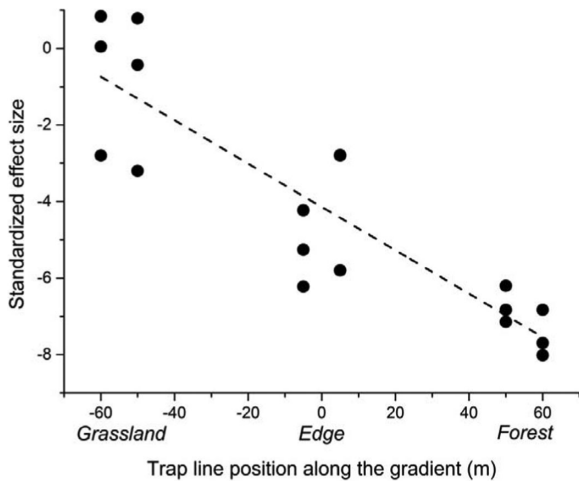
The pairwise functional and phylogenetic distance values were significantly correlated (Mantel test,  $R = 0.2531$ ,  $P < 0.001$ ), indicating that the more closely related species have more similar traits (trait conservatism).

We found that the standardized effect sizes were negatively correlated with the position along the grassland–forest gradient for all values of the phylogenetic-weighting parameter ( $a$ ), which means that environmental conditions in forested habitats (forest edges and interiors) strongly selected for assemblages of functionally and phylogenetically similar species. The variance explained by the position along the gradient was maximized at a low value of the phylogenetic-weighting parameter,  $a = 0.125$  (maximal  $R^2_{\text{adjusted}} = 0.703$ , Figs. 1 and 2). Moreover, the variance steeply decreased at  $a > 0.6$  (Fig. 1). This suggested that combining functional and phylogenetic information better revealed the effects of community assembly mechanisms along the studied gradient than the 2 components evaluated separately, although the weight of the phylogenetic component was minimal.

The mean standardized effect sizes in grassland assemblages, calculated for  $a = 0.125$  were not significantly different from zero, indicating a randomly structured ground beetle assemblage (Fig. 3). However, assemblages in both the forest edge and interior were significantly clustered (underdispersed), both by functional and phylogenetic measures, suggesting that co-occurring species were more closely related and functionally more



**Fig. 1** The strength of relationship (expressed as  $R^2_{\text{adjusted}}$ ) between the standardized effect sizes and the position along the grassland–forest gradient for 41 levels of the functional–phylogenetic weighting parameter ( $a$ ) from 0 to 1 by increasing  $a$  in steps of 0.025.

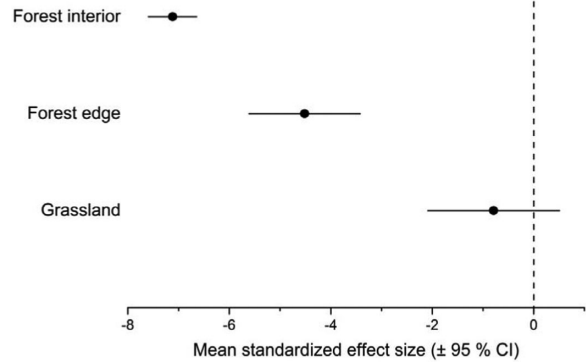


**Fig. 2** The significant negative linear relationship ( $F = 41.15$ ,  $df = 1,16$ ,  $P < 0.0001$ ,  $R^2_{\text{adjusted}} = 0.7025$ ) between the standardized effect sizes and the position along the grassland–forest gradient at the phylogenetic-weighting parameter of  $a = 0.125$ .

similar than expected by chance, which is an indication environmental filtering (Fig. 3).

**Discussion**

Ground beetle assemblages in the studied grassland habitat were randomly structured, and did not seem to be influenced by either environmental filtering or species interactions. Contrary to our findings, environmental filtering was the main community assembly process for



**Fig. 3** The mean standardized effect sizes calculated with a phylogenetic-weighting parameter value of  $a = 0.125$  ( $\pm 95\%$  confidence interval) in the studied habitats along the grassland–forest gradient.

nonvolant small mammals in grassland, as closely related and ecologically similar species coexisted (phylogenetic and morphological clustering; Luza *et al.* 2015). Debastiani *et al.* (2015) also reported such clustering for woody plant species in Brazilian grasslands, indicating environmental filtering. The main explanation for the observed random structure in our studied grassland patches is the asymmetrical species flow (spillover) across the forest edge (Magura, 2017). Forest edges maintained by natural processes (such as the studied ones) are penetrable for forest species, allowing them to move right through the edges and to disperse into the neighboring open habitats, while these same edges are inhospitable for grassland species (both open-habitat and generalist ones), preventing them to penetrate into the forest interior (Magura *et al.*, 2017). Asymmetrical species flow of ground beetles between open habitats and neighboring forests regularly occurs (Magura *et al.*, 2001; Koivula *et al.*, 2004; Roume *et al.*, 2011; Brigić *et al.*, 2014; Lacasella *et al.*, 2015; Boetzl *et al.*, 2016; Schneider *et al.*, 2016; Yekwayo *et al.*, 2017), allowing the coexistence of grassland species and functionally and phylogenetically dissimilar forest species in the grassland.

Co-occurring species in the forest edge were more closely related and functionally more similar than expected by chance, indicating environmental filtering. Similarly, as it was hypothesized, co-existing ground beetle species in the forest interior were also functionally and phylogenetically clustered. The underlying mechanisms for these patterns may be the asymmetrical species flow across edges and strong environmental filtering. As a consequence, few open-habitat and generalist species from the adjacent grassland move into the forest edge and

almost none of these cross the edge into the forest interior (Magura, 2017; Magura *et al.*, 2017). The environmental filtering, both at the forest edge and in the interior, leads to communities composed of closely related, predominantly forest species with phylogenetically conserved traits. The key filter condition could be high humidity and/or a low temperature, as both are among the most important environmental parameters influencing spatial distribution and persistence of not only the ground beetle adults, but especially the larvae that have limited mobility, weak chitinization, and therefore narrower tolerance limits than adults (Lövei & Sunderland, 1996). Another key factor for filtering co-existing species in the forest edge and interior could be the thick leaf litter layer, as it offers prey, habitat space and shelter from adverse microclimatic conditions (Koivula *et al.*, 1999; Magura *et al.*, 2001; Taboada *et al.*, 2004; Skłodowski, 2014). While environmental filtering acted on ground beetles at the studied forest edge, in the case of nonvolant small mammals in southern Brazil, phylogenetically similar species coexisted less often than expected by chance, indicating a repulsion pattern (Luza *et al.*, 2015). Community assembly processes at the forest edge can be different depending on the dispersal ability of the various taxa. Smaller and/or less mobile animals generally use fewer different microhabitats and may interact less frequently with other species than larger or more mobile ones that use more types of microhabitats (Pianka, 2011). There is no such discrepancy in the forest interior: closely related and ecologically similar nonvolant small mammals (Luza *et al.*, 2015) and woody plant species (Debastiani *et al.*, 2015) also can coexist, similar to our findings for ground beetles.

Our results showed that species interactions (competition) did not contribute to the organization of the studied ground beetle communities. The importance and generality of competition among co-occurring ground beetle species in structuring communities has been long debated (den Boer, 1989; Niemelä, 1993). Food limitation exists both in the larval (Nelemans, 1988) and the adult stages (Lenski, 1984; Bilde & Toft, 1998) under field conditions. Based on these data, it might be assumed that species interactions (competition) should be key factors for community assembly of ground beetles especially in heterogeneous, structurally complex habitats with ample resources (such as forest edges), since resource concentration, structural complexity and habitat heterogeneity promote colonization by a wider range of species (Blakely & Didham, 2010). In these habitats, low similarity between species might be expected due to effective niche partition. Using a phylogenetically based null model, Barraclough *et al.* (1999) tested whether co-occurring tiger beetles of a monophyletic subgenus had lower than

expected similarity in mandible size. These authors, however, found no evidence for character divergence between co-occurring species, that is, similarly to our results, species interactions do not play an important role in community assembly (Barraclough *et al.*, 1999). They concluded that the effects of interactions among members of the studied subgenus might be obscured by interactions with the other subgenus, or the strength of interactions may be weak compared to environmental filtering (Barraclough *et al.*, 1999). Currently there is no convincing evidence that competition has an important role in ground beetle community assembly. Even manipulative experiments were not able to provide satisfying evidence for interspecific competition as a regulatory force in communities (Loreau, 1990; Niemelä, 1993). Microhabitat selection (e.g., vertical separation of the co-existing species in thick deciduous litter layer; Loreau, 1987) and diurnal or seasonal changes in activity may be important strategies to avoid interspecific competition, permitting phylogenetically and functionally similar ground beetle species to coexist. Also resource (prey and other food sources) partitioning might contribute to species co-existence as there are clear differences in body size (mandible size) among co-existing species (e.g., predatory *Carabus* and *Pterostichus* species, Magura *et al.*, 2000). Intense competition takes place instead between ground beetles and other ground-dwelling generalist predators, like spiders and ants (Lövei & Sunderland, 1996).

Our results, which showed that environmental filtering is the main assembly rule in the forest edge and interior in a forest without human management, have an important conservation message. Among terrestrial ecosystems, natural forests including their edges support the greatest share of the global biodiversity (Lindenmayer *et al.*, 2006), and thus the conservation of forest biodiversity is a vital task (Paillet *et al.*, 2010). Forest edges also have important functions regulating dispersal or invisibility (Ries *et al.*, 2004). Edges maintained mainly by natural processes inhibit the open-habitat and generalist species to penetrate into the forest interior (Magura *et al.*, 2017). Unfavorable, human-induced changes to their structure, composition and characteristics may alter their filter function, make them permeable, allowing the species from the surrounding, nonforested habitats to colonize the forest interior (Cadenasso and Pickett, 2001; Strayer *et al.*, 2003; Magura *et al.*, 2017). Invasion by open-habitat and generalist species may cause the decline or local extinction of native forest specialists and facilitate or accelerate further invasion by alien species, that may lead to invasional meltdown (Green *et al.*, 2011) and/or further habitat deterioration both in the edge and the interior (Murcia, 1995;

Harper *et al.*, 2005, 2015;). Therefore, to avoid damage to biodiversity and the functioning of forest edges and interiors, protecting the integrity of natural forest edges is an important task in conservation management.

## Conclusion

Earlier studies have demonstrated that ground beetle communities along the grassland–forest edge–forest interior gradient differ in terms of species composition and taxonomic diversity (Magura, 2002; Tóthmérész *et al.*, 2014; Ohwaki *et al.*, 2015), but also functional and phylogenetic diversity (Magura, 2017). This study, however, allows a deeper insight into the mechanisms driving assembly processes than previously. We showed that combining functional and phylogenetic information helped to understand the community assembly mechanisms more than the 2 components evaluated separately, even though in the studied situation, the weight of the phylogenetic component was small. Our study revealed that differences in composition and diversity along grassland–forest edge–forest gradients were accompanied by strong shifts in the phylogenetic and functional diversity, with possible consequences for ecosystem functioning. While only from a limited number of sites in a similar landscape, and thus in need of confirmation from other locations, our results indicated that different community assembly of ground beetles existed on opposite sides of the forest edge. Stochastic (random) processes were the assembly rule structuring ground beetle community in the grassland, while environmental filtering was important in the forest interior and at the forest edge. Both community assembly rules were considerably affected by asymmetrical species flow (spillover) across the forest edge, underlining the filter function of forest edges.

## Acknowledgments

We thank Tivadar Molnár for his help during the field and laboratory work, and 2 anonymous reviewers for their thoughtful comments. This publication was supported by the SROP4.2.2.B15/1/KONV20150001 project, financed by the European Union and the European Social Fund.

## Disclosure

There was no financial or other commitment that might potentially bias our work and we declare no conflict of interest.

## References

- Barbaro, L., Giffard, B., Charbonnier, Y., van Halder, I. and Brockerhoff, E.G. (2014) Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. *Diversity and Distributions*, 20, 149–159.
- Barracough, T.G., Hogan, J.E. and Vogler, A.P. (1999) Testing whether ecological factors promote cladogenesis in a group of tiger beetles (Coleoptera: Cicindelidae). *Proceedings of the Royal Society B: Biological Sciences*, 266, 1061.
- Bässler, C., Müller, J., Cadotte, M.W., Heibl, C., Bradtka, J.H., Thorn, S. *et al.* (2016) Functional response of lignicolous fungal guilds to bark beetle deforestation. *Ecological Indicators*, 65, 149–160.
- Belinchón, R., Martínez, I., Aragón, G. and Escudero, A. (2012) Lichen species co-occurrence patterns along an edge-interior Mediterranean forest gradient. *Acta Oecologica*, 43, 150–157.
- Beutel, R.G., Ribera, I. and Bininda-Emonds, O.R.P. (2008) A genus-level supertree of Adephaga (Coleoptera). *Organisms Diversity and Evolution*, 7, 255–269.
- Bilde, T. and Toft, S. (1998) Quantifying food limitation of arthropod predators in the field. *Oecologia*, 115, 54–58.
- Blakely, T.J. and Didham, R.K. (2010) Disentangling the mechanistic drivers of ecosystem-size effects on species diversity. *Journal of Animal Ecology*, 79, 1204–1214.
- Boetzel, F.A., Schneider, G. and Krauss, J. (2016) Asymmetric carabid beetle spillover between calcareous grasslands and coniferous forests. *Journal of Insect Conservation*, 20, 49–57.
- Bogyó, D., Magura, T., Nagy, D.D. and Tóthmérész, B. (2015) Distribution of millipedes (Myriapoda, Diplopoda) along a forest interior–forest edge–grassland habitat complex. *ZooKeys*, 510, 181–195.
- Brigić, A., Starčević, M., Hrašovec, B. and Elek, Z. (2014) Old forest edges may promote the distribution of forest species in carabid assemblages (Coleoptera: Carabidae) in Croatian forests. *European Journal of Entomology*, 111, 715–725.
- Cadenasso, M.L. and Pickett, S.T.A. (2001) Effect of edge structure on the flux of species into forest interiors. *Conservation Biology*, 15, 91–97.
- Cadenasso, M.L., Pickett, S.T. A., Weathers, K.C. and Jones, C.G. (2003) A framework for a theory of ecological boundaries. *BioScience*, 53, 750–758.
- Cadotte, M., Albert, C.H. and Walker, S.C. (2013) The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecology Letters*, 16, 1234–1244.
- Cadotte, M.W., Jonathan Davies, T., Regetz, J., Kembel, S.W., Cleland, E. and Oakley, T.H. (2010) Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecology Letters*, 13, 96–105.

- D’Orazio, M., Di Zio, M. and Scanu, M. (2006) *Statistical Matching: Theory and Practice*. John Wiley & Sons, Chichester. pp. 268.
- Davison, A.C. and Hinkley, D. V. (1997) *Bootstrap Methods and Their Applications*. Cambridge University Press, Cambridge. pp. 592.
- Debastiani, V.J., Muller, S.C., Oliveira, J.M., Fernando, S., Sestren-Bastos, M.C. and Duarte, L.D.S. (2015) Recurrent patterns of phylogenetic habitat filtering in woody plant communities across phytogeographically distinct grassland-forest ecotones. *Community Ecology*, 16, 1–9.
- Den Boer, P.J. (1989) Comment on the article “On testing temporal niche differentiation in carabid beetles” by M. Loreau. *Oecologia*, 81, 97–98.
- Digweed, S.C., Currie, C.R., Carcamo, H.A. and Spence, J.R. (1995) Digging out the digging-in effect of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia*, 39, 561–576.
- Dodonov, P., da Silva, D.M. and Rosatti, N.B. (2014) Understorey vegetation gradient in a Eucalyptus grandis plantation between a savanna and a semideciduous forest. *New Zealand Journal of Forestry Science*, 44, 10.
- Dray, S. and Dufour, A.B. (2007) The ade4 Package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20.
- Elek, Z. and Tóthmérész, B. (2011) Carabid beetles among grassland—forest edge—beech forest habitats in Northern Hungary. *Community Ecology*, 11, 211–216.
- Forman, R.T.T. and Godron, M. (1986) *Landscape Ecology*. Wiley & Sons, New York. pp. 640.
- Gerisch, M. (2014) Non-random patterns of functional redundancy revealed in ground beetle communities facing an extreme flood event. *Functional Ecology*, 28, 1504–1512.
- Gerlach, J., Samways, M. and Pryke, J. (2013) Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation*, 17, 831–850.
- Gower, J.C. (1971) A general coefficient of similarity and some of its properties. *Biometrics*, 27, 857–871.
- Green, P.T., O’Dowd, D.J., Abbott, K.L., Jeffery, M., Retallick, K. and Mac Nally, R. (2011) Invasional meltdown: invader–invader mutualism facilitates a secondary invasion. *Ecology*, 92, 1758–1768.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D. *et al.* (2015) Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances*, 1, 1–9.
- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosnokske, K.D., Saunders, S.C. *et al.* (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, 19, 768–782.
- Harper, K.A., Macdonald, S.E., Mayerhofer, M.S., Biswas, S.R., Esseen, P.-A., Hylander, K. *et al.* (2015) Edge influence on vegetation at natural and anthropogenic edges of boreal forests in Canada and Fennoscandia. *Journal of Ecology*, 103, 550–562.
- Heikkala, O., Seibold, S., Koivula, M. *et al.* (2016) Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. *Forest Ecology and Management*, 359, 51–58.
- Hubbell, S.P. (2006) Neutral theory and the evolution of ecological equivalence. *Ecology*, 87, 1387–1398.
- Hürka, K. (1996) *Carabidae of the Czech and Slovak Republics*. Kabourek, Zlin. pp. 565.
- Kapos, V. (1989) Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology*, 5, 173–185.
- Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, 3, 157–164.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D. *et al.* (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464.
- Koch, K. (1989) *Die Käfer Mitteleuropas. Ökologie*. Goecke & Evers Verlag, Krefeld. pp. 440.
- Koivula, M., Hyyryläinen, V. and Soininen, E. (2004) Carabid beetles (Coleoptera: Carabidae) at forest-farmland edges in southern Finland. *Journal of Insect Conservation*, 8, 297–309.
- Koivula, M., Punttila, P., Haila, Y. and Niemelä, J. (1999) Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography*, 22, 424–435.
- Lacasella, F., Gratton, C., De Felici, S., Isaia, M., Zapparoli, M., Marta, S. *et al.* (2015) Asymmetrical responses of forest and ‘beyond edge’ arthropod communities across a forest-grassland ecotone. *Biodiversity and Conservation*, 24, 447–465.
- Larochelle, A. (1990) The food of the carabid beetles (Coleoptera: Carabidae, including Cicindelinae). *Faberies*, Suppl. 5, 1–132.
- Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ribeiro, J.E.L.S., Giraldo, J.P. *et al.* (2006) Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 19010–19014.
- Lenski, R.E. (1984) Food limitation and competition: a field experiment with two Carabus species. *Journal of Animal Ecology*, 53, 203–216.
- Lindenmayer, D.B., Franklin, J.F. and Fischer, J. (2006) General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation*, 131, 433–445.
- Loreau, M. (1987) Vertical distribution of activity of carabid beetles in a beech forest floor. *Pedobiologia*, 30, 173–178.



- Loreau, M. (1990) Competition in a carabid beetle community: a field experiment. *Oikos*, 58, 25–38.
- Lövei, G.L., Magura, T., Tóthmérész, B. and Ködöböcz, V. (2006) The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands. *Global Ecology and Biogeography*, 15, 283–289.
- Lövei, G.L. and Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, 41, 231–256.
- Luza, A.L., Gonçalves, G.L. and Hartz, S.M. (2015) Phylogenetic and morphological relationships between nonvolant small mammals reveal assembly processes at different spatial scales. *Ecology and Evolution*, 5, 889–902.
- Ma, M. and Herzon, I. (2014) Plant functional diversity in agricultural margins and fallow fields varies with landscape complexity level: conservation implications. *Journal for Nature Conservation*, 22, 525–531.
- Magura, T. (2002) Carabids and forest edge: spatial pattern and edge effect. *Forest Ecology and Management*, 157, 23–37.
- Magura, T. (2017) Ignoring functional and phylogenetic features masks the edge influence on ground beetle diversity across forest-grassland gradient. *Forest Ecology and Management*, 384, 371–377.
- Magura, T., Bogyó, D., Mizser, S., Nagy, D.D. and Tóthmérész, B. (2015) Recovery of ground-dwelling assemblages during reforestation with native oak depends on the mobility and feeding habits of the species. *Forest Ecology and Management*, 339, 117–126.
- Magura, T., Lövei, G.L. and Tóthmérész, B. (2017) Edge responses are different in edges under natural versus anthropogenic influence: a meta-analysis using ground beetles. *Ecology and Evolution*, 7, 1009–1017.
- Magura, T., Tóthmérész, B. and Molnár, T. (2000) Spatial distribution of carabids along grass-forest transects. *Acta Zoologica Academiae Scientiarum Hungaricae*, 46, 1–17.
- Magura, T., Tóthmérész, B. and Molnár, T. (2001) Forest edge and diversity: carabids along forest-grassland transects. *Biodiversity and Conservation*, 10, 287–300.
- Máthé, I. (2006) Forest edge and carabid diversity in a Carpathian beech forest. *Community Ecology*, 7, 91–97.
- Matlack, G. (1994) Vegetation dynamics of the forest edge—trends in space and successional time. *Journal of Ecology*, 82, 113–123.
- Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, 10, 58–62.
- Nelemans, M.N.E. (1988) Surface activity and growth of larvae of *Nebria brevicollis* (F.) (Coleoptera, Carabidae). *Netherlands Journal of Zoology*, 38, 74–95.
- Niemelä, J. (1993) Interspecific competition in ground-beetle assemblages (Carabidae): what have we learned? *Oikos*, 66, 325–335.
- Ohwaki, A., Kaneko, Y. and Ikeda, H. (2015) Seasonal variability in the response of ground beetles (Coleoptera: Carabidae) to a forest edge in a heterogeneous agricultural landscape in Japan. *European Journal of Entomology*, 112, 135–144.
- Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M. et al. (2010) Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conservation Biology*, 24, 101–112.
- Pausas, J.G. and Verdú, M. (2010) The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *BioScience*, 60, 614–625.
- Peralta, G., Frost, C.M., Didham, R.K., Varsani, A. and Tylianakis, J.M. (2015) Phylogenetic diversity and co-evolutionary signals among trophic levels change across a habitat edge. *Journal of Animal Ecology*, 84, 364–372.
- Pianka, E.R. (2011) *Evolutionary Ecology*, Eric R. Pianka.
- R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Ries, L., Fletcher, R.J., Battin, J. and Sisk, T.D. (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution and Systematics*, 35, 491–522.
- Ries, L. and Sisk, T.D. (2004) A predictive model of edge effects. *Ecology*, 85, 2917–2926.
- Roume, A., Deconchat, M., Raison, L., Balent, G. and Ouin, A. (2011) Edge effects on ground beetles at the woodlot-field interface are short-range and asymmetrical. *Agricultural and Forest Entomology*, 13, 395–403.
- Schlinkert, H., Ludwig, M., Batáry, P., Holzschuh, A., Kovács-Hostyánszki, A., Tscharrntke, T. et al. (2016) Forest specialist and generalist small mammals in forest edges and hedges. *Wildlife Biology*, 22, 86–94.
- Schneider-Maunoury, L., Lefebvre, V., Ewers, R.M., Medina-Rangel, G.F., Peres, C.A., Somarriba, E. et al. (2016) Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forest landscapes. *Biological Conservation*, 200, 207–215.
- Schneider, G., Krauss, J., Boetzi, F.A., Fritze, M.A. and Steffan-Dewenter, I. (2016) Spillover from adjacent crop and forest habitats shapes carabid beetle assemblages in fragmented semi-natural grasslands. *Oecologia*, 182, 1141–1150.
- Skłodowski, J. (2014) Consequence of the transformation of a primeval forest into a managed forest for carabid beetles (Coleoptera: Carabidae)—a case study from Białowieża (Poland). *European Journal of Entomology*, 111, 639–648.
- Spake, R., Barsoum, N., Newton, A.C. and Doncaster, C.P. (2016) Drivers of the composition and diversity of carabid functional traits in UK coniferous plantations. *Forest Ecology and Management*, 359, 300–308.

- Strayer, D.L., Power, M.E., Fagan, W.F., Pickett, S.T.A. and Belnap, J. (2003) A classification of ecological boundaries. *BioScience*, 53, 723–729.
- Swenson, N.G. (2013) The assembly of tropical tree communities—the advances and shortcomings of phylogenetic and functional trait analyses. *Ecography*, 36, 264–276.
- Taboada, A., Kotze, D.J. and Salgado, J.M. (2004) Carabid beetle occurrence at the edges of oak and beech forests in NW Spain. *European Journal of Entomology*, 101, 555–563.
- Terraube, J., Archaux, F., Deconchat, M., van Halder, I., Jactel, H. and Barbaro, L. (2016) Forest edges have high conservation value for bird communities in mosaic landscapes. *Ecology and Evolution*, 6, 5178–5189.
- Tóthmérész, B., Nagy, D.D., Mizser, S., Bogyó, D. and Magura, T. (2014) Edge effects on ground-dwelling beetles (Carabidae and Staphylinidae) in oak forest-forest edge-grassland habitats in Hungary. *European Journal of Entomology*, 111, 686–691.
- Turner, M.G., Gardner, R.H. and O'Neill, R.V. (2001) *Landscape Ecology in Theory and Practice. Pattern and Process*. Springer, New York. pp. 401.
- Vellend, M. (2010) Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, 85, 183–206.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. and Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505.
- Yekwayo, I., Pryke, J.S., Roets, F. and Samways, M.J. (2016) Conserving a variety of ancient forest patches maintains historic arthropod diversity. *Biodiversity and Conservation*, 25, 887–903.
- Yekwayo, I., Pryke, J.S., Roets, F. and Samways, M.J. (2017) Responses of ground living arthropods to landscape contrast and context in a forest-grassland mosaic. *Biodiversity and Conservation*, 26, 631–651.

Manuscript received April 28, 2017

Final version received June 20, 2017

Accepted June 27, 2017