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Edge history modulates the depth of edge influence: Evidence from ground beetles with different feeding traits

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ABSTRACT

Anthropogenic habitat loss and fragmentation are major concerns to conservationists, since these processes lead to species decline and extinction. Edge effect is one of the most important causes of biodiversity losses in fragmented habitats. The depth of edge influence, the distance over which the edge effect penetrates into the adjacent habitat is a central issue, as it fundamentally determines whether the habitat fragment has any remaining core habitat, which is essential for the survival of habitat specialist species. We reviewed 204 edge studies on ground beetles (Coleoptera: Carabidae) of different feeding habits, in forests, one of the habitats most impacted by humans. Meta-analysing 1814 abundance data of 351 ground beetle species from forest edges and their adjoining interiors, we showed that forest edges had significantly higher abundance of herbivorous, omnivorous, and predatory ground beetles than their interiors. Edge history considerably affected the depth of edge influence which on all trophic groups was similar in natural edges and those maintained by agriculture (≤ 10–20 m), while it was wider (> 300 m) when created by forestry or other anthropogenic activities. Consequently, the minimum area of a forest fragment should be ∼ 330 ha in order to keep half of it as core habitat to preserve forest-interior species.

1. Introduction

Humans have by today colonised all habitats and have transformed most of them (Ellis, 2011). Forests are one of the habitat types most impacted by humans (López-Bedoya et al., 2021; Paillet et al., 2010). For example, in Europe, 46% of the land surface is forested, but only ∼2% of this is composed of intact, natural forests (Keenan et al., 2015). These habitat-transforming activities commonly cause fragmentation as well as a reduction of the area of the original, natural habitats. These two, often concurrent effects (reducing the area as well as fragmenting the remainder) create new landscapes with lots more edges than what would form naturally. The prevalence of edges and consequently, the magnitude of edge effects has increased due to human activities (Fletcher, 2005; López-Barrera et al., 2007; Watkins et al., 2003). Edge effects and understanding of their driving mechanisms are globally becoming more and more important (Ruffell and Didham, 2016).

Landscapes are usually composed of a major component (a matrix) and smaller areas, fragments of other types of habitats. Due to anthropogenic landscape transformation, the fragments are often composed of the remainders of the original, natural habitat – the original matrix that has now been fragmented. Edges often "intrude" into these fragments, and the usual effect is to degrade their original features, making them more similar to matrix conditions, or create a transitional zone where many of the original habitat conditions cease to exist. In case of an originally forested region, this process means a reduction of the remaining area covered by forest, as well as the creation of forest fragments of various sizes. In fragments, the edge-to-interior ratio is significantly increased, with the environmental conditions in the edge being considerably different from those in the interior (Ries et al., 2004). The question emerges what happens to the inhabitants of the original, now fragmented habitat? What are the consequences for those that require the original conditions, how do they react to the increased area of edges, and to the eventual arrival of new species, be those edge specialists or matrix inhabitants?

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This is a non-trivial question because the new matrix is often anthropogenic, and not suitable for supporting the original flora and fauna. As follows from the theory of island biogeography (MacArthur and Wilson, 1967), the bigger the remaining area of the original matrix, even if now fragmented, the smaller is the loss of its original biodiversity. Edge effects are a key determinant, since most effects of fragmentation attributed to patch area may be scaled-up edge effects (Banks-Leite et al., 2010; Murphy et al., 2016). In this context, the extent of the edge is important to determine the effective area of the remaining original habitat.

The forest edge is a transition zone where the forest habitat and the surrounding matrix interact, channelling flows of energy, nutrients and species (Murcia, 1995; Ries et al., 2004), with consequent changes in the abiotic environmental parameters, as well as in the composition and structure of the inhabiting biological communities (Harper et al., 2005; Murcia, 1995). Gradual changes in environmental conditions from the forest edge towards the interior (abiotic edge effect; Murcia, 1995) include well documented changes in solar radiation (Harper et al., 2005; Kapos, 1989), wind speed and air turbulence (Davies-Colley et al., 2000), air humidity (Kapos, 1989), soil moisture (Riutta et al., 2012), and air and soil temperature (Bogyó et al., 2015). These also influence ecosystem processes such as photosynthesis (Leme et al., 2021), regeneration (Šálek et al., 2013), nutrient cycling (Vasconcelos and Luizão, 2004), and decomposition (Riutta et al., 2012). Edges may be subjected to the deposition of ammonium, nitrates and sulphates from the neighbouring matrix (Wuyts et al., 2008). Such changes in microclimate, chemical inputs, and ecosystem processes result in edge-interior differences in top soil properties, and undergrowth plant species composition and structure (Matlack, 1994; Wuyts et al., 2011). Variation in plant species composition and structure at forest edges may also influence their animal species composition (direct biological edge effect; Murcia, 1995), leading to changes in species interactions near the edge (indirect biological edge effect; Murcia, 1995). These abiotic and biotic changes can extend far inside the forest patch, meaning that the edge effect can be considerable (Ewers and Didham, 2008; Harper and Macdonald, 2001; Murcia, 1995).

The depth of edge influence (DEI; Ries et al., 2004) is a central issue in edge studies. Several papers determined DEI for abiotic (e.g. Saunders et al., 1999), as well as biotic parameters (e.g. Tsafack et al., 2023), and ecological processes (e.g. Riutta et al., 2016). Studies on DEI concerning species traits, however, are rather limited (but see Labadessa et al., 2017), although to understand the functioning of ecological processes without considering species traits is hardly possible (Caitano et al., 2020). DEI is influenced by various habitat characteristics (size, shape, isolation, type and quality of adjacent habitats, orientation, temporal effects, edge contrast; Ewers and Didham, 2006; Nguyen and Nansen, 2018; Peyras et al., 2013; Ries et al., 2004) and by species traits (Peyras et al., 2013). Forest edges also differ in their origin and maintaining processes, and the age, history, and origin of edges can also be important drivers of DEI (Harper et al., 2015; Strayer et al., 2003). Forest edges maintained by natural processes (succession, irregular extensive grazing, and irregular mowing) versus edges repeatedly disturbed and maintained by anthropogenic activities (forestry, agriculture, urbanization) have different structural and functional characteristics and have different filter function (history-based edge effect hypothesis; Magura et al., 2017). Forest edges maintained by natural processes have a stratified horizontal structure, making them less permeable, inhibiting the extensive influx of species from the adjacent (usually non-forested) matrix into the forest interior. In contrast, edges still under anthropogenic influence have a simplified horizontal structure, and are permeable, allowing elements from the matrix to penetrate deep into the forest interior. This effect may decrease with time if edges undergo a natural development ("edge sealing"; Williams-Linera, 1990).

In this study we sought to examine the edge responses of a common, species-rich group of ground-active arthropods, ground beetles (Coleoptera: Carabidae). We used published information on ground beetle species, and sought to quantify the DEI on species with different feeding habits in forest edges. Ground beetles were selected as study objects because their taxonomy and traits including feeding habit are well known, they are common and abundant in most terrestrial habitats and thus may have an important ecological role in ecosystems (Lövei and Sunderland, 1996), and there are sufficient data from edge studies to make them suitable for testing their edge responses (Magura et al., 2017). Edge history and the nature of contrast between a forest fragment and its surrounding matrix are important factors to determine the reaction of both forest specialists and matrix generalists to forest fragmentation. Forest edges maintained by natural processes have higher carabid species richness, while those under continued anthropogenic influence do not (Magura et al., 2017). A forest fragment with an anthropogenic edge is vulnerable to invasion by macropterous open-habitat species, while natural forest edges are impenetrable for them (Magura and Lövei, 2020b). During fragmentation, the surviving forest specialists will have smaller body sizes (Magura et al., 2020). In the present study we focused how trophic position (feeding habit) modulates the DEI in forest fragments and their edges. Our further motivation was that although there are arthropod studies on DEI in forests (e.g. for ground beetles: Noreika and Kotze, 2012; for spiders: Hogg and Daane, 2011), and even on DEI across various edges (natural vs. anthropogenic) in a narrow geographic region (for spiders: Larrivée et al., 2008), to our knowledge there are no studies (systematic reviews or meta-analyses) at wider scales that compare DEI in edges maintained by natural processes versus anthropogenic influences using the same arthropod group. Specifically, we hypothesised (1) that due to a wider range of environmental conditions near edges and related increases of resources (Ries et al., 2004), the abundance of ground beetle species at both lower (herbivore) and higher (omnivore, predator) trophic levels should be higher in forest edges than interiors. We defined DEI as the distance into the forest until such an abundance did not significantly change. We also hypothesised (2) that the structural and functional properties of edges should modulate the DEI, creating wider edges under continued anthropogenic influence than those maintained by natural processes. We found support for both hypotheses: the abundance of herbivorous, omnivorous, and predatory ground beetles was significantly higher at the edges of forest fragments than in their interiors. Furthermore, DEI was larger in fragments whose edges were repeatedly disturbed and maintained by anthropogenic activities.

2. Material and methods

2.1. Literature search and compilation of data sets

We re-evaluated the continuously updated dataset collected for earlier studies on edges (Magura et al., 2017; Magura and Lövei, 2020b). We included only those studies that reported data on mean ground beetle abundance at least at a clearly defined forest interior and a forest edge, where we could also find data on the distance from the edge. Data were extracted from text, tables, and figures.

2.2. Classification of species and edges

Species at different trophic levels may show different edge responses; therefore, ground beetle species, for which we extracted abundance data, were classified by their diet based on literature data (Larochelle, 1990), distinguishing

(1) herbivores (the main component of their diet is plant material, including seeds),
(2) omnivores (or mixed feeders consuming both plant and animal material), and
(3) predators (feeding on animal material).

These categories represent both lower (herbivore) and higher (omnivore, predator) trophic levels. Subsequently, data on herbivorous, omnivorous, and predatory species were evaluated separately.

Forest edges have different structural characteristics when maintained by natural processes or by anthropogenic activities (Strayer et al., 2003). Forest edges maintained by natural processes are well structured, and have stratified horizontal vegetation layers (Forman and Godron, 1986). Contrarily, edges subjected to repeated anthropogenic activities (including forestry operations, management of the urban environment, tillage, pesticide, herbicide and fertilizer use, intensive grazing, mowing, repeated fires) have a simplified horizontal vegetation structure. This difference has consequences for population, community, and ecosystem structures, and change resource availability, substrate structure, and/or the physical environment (Pickett and White, 1985). Edges with such distinct horizontal structures have fundamentally different functional characteristics and filter function (Magura et al., 2017).

Therefore, forest edges were classified based on their origin and maintaining processes. Edges were considered to be maintained by natural processes when their forest interiors were without regular fire events, cutting or thinning, and adjacent grasslands were not regularly burnt, mowed or intensively grazed for at least 50 years. These edges may be subjected to irregular, non-intensive management interventions (occasional mowing and/or low-intensity grazing), with succession starting between such disturbance events (Magura et al., 2017). On the other hand, edges under continued anthropogenic influence were created by forestry activities (e.g. clear-cutting), urbanization or agriculture, and their neighbouring habitats were cultivated or intensively grazed, mowed, and/or regularly burned.

2.3. Depth of edge definitions

To quantify the DEI, sampling locations in the forest interiors were grouped into distance classes: (1) 0–5 m from the edge, (2) 5–10 m from the edge, (3) 10–20 m from the edge, (4) 20–50 m from the edge, and (5) $>$ 50 m from the edge. During the calculations, distance classes with $n<4$ were excluded from further analyses (for details see Table S3). DEI was determined as the distance over which there was no significant difference between the mean abundances at the sampling location and the interior. If there was no significant difference between the mean abundance at the forest edge and the interior sites at $>$ 50 m from the edge, then sampling locations in this distance class were further divided if possible, into subclasses with interior sampling locations at 50–100 m, and 100–300 m from the edge to more precisely detect DEI.

2.4. Statistical analyses

Recently, Spake and Doncaster (2017) recommended using a response ratio for calculating the effect size in forest biodiversity research, as their use can overcome the differences between studies in design and quality, spatial configuration, and geographical distribution. Therefore, to get a more robust and general response pattern, we quantified the edge response of species using the relative interaction intensity (*RII*, Armas et al., 2004). In our data set, *RII* measured the difference between the mean abundances in the forest interior and the forest edge, standardized by the total mean number of individuals collected. *RII* was calculated as

$$RII = \left(X_{Forest} - X_{Edge}\right) / \left(X_{Forest} + X_{Edge}\right),$$

where X_{Forest} was the mean abundance of a species in the forest interior, and X_{Edge} was the mean abundance at the forest edge. This effect size is symmetrical, gives positive and negative responses equally, and has no discontinuities (Armas et al., 2004). In our situation, positive values of *RII* indicated higher abundance in the forest interior than at the edge, while negative values indicated the opposite. *RII* has several features that make it favourable to calculate effect size in meta-analyses. Its calculation is based on means alone; therefore studies that did not report variances but met all other inclusion criteria could be included. *RII* has a straight-forward interpretation, as it quantifies the edge response of species relative to the nearby forest interior. Furthermore, *RII* and the classic log response ratio (*LRR*, Hedges et al., 1999) are formally related because *LRR* is a special case of *RII* (Armas et al., 2004). *LRR*, however, has the disadvantage that it cannot be calculated if either of the two means is zero, while *RII* does not suffer from this limitation. This is advantageous because omitting studies with zero individuals at either end of the interior - edge gradient can cause bias in the meta-analysis by excluding species with the most extreme responses (Armas et al., 2004). Based on the above features, *RII* is frequently used in meta-analysis (e.g. Martinson and Raupp, 2013).

To determine significant differences between the mean abundance of species in the forest edge and interior, the *RII* with bootsrapped confidence intervals (with 999 iterations) was calculated using the *boot* package (Canty and Ripley, 2022; Davison and Hinkley, 1997) We considered the effect size to be significantly different from zero if the confidence intervals did not include zero. All calculations were done in the R 4.2.1 environment (R Core Team, 2023).

3. Results

3.1. Evidence structure

The literature search yielded 204 publications. After assessing whether these papers meet selection criteria, we compiled a data set of average species abundances at the forest interior and forest edge from a total of 44 publications (Figure S1). Twelve papers studied natural forest edges, and 31 papers investigated anthropogenic ones; one study examined both. Edges maintained by human influence were further grouped according to the activity: agriculture (14 papers), forestry (11 papers), and others (industry, recreation, or urbanization; 5 papers). Two papers studied both forestry and urbanization (Table S1). Studies were mostly from Europe (24 papers) and North America (8); one paper presented data from both. The number of experiments from Asia (5) and South America (4) were smaller, and only two papers reported work from Australia (Table S1). From these papers, we recorded 1814 abundance comparisons (rows in our data set) of 351 ground beetle species. Most of these (277 species) were classified as predators; 23 were herbivorous and 51 omnivorous (Table S2). From these 1814 comparisons, only 631 presented mean abundance, standard deviations and sample sizes (Table S3). Thus, approximately two-thirds of the extracted data would be unusable if the effect size using the standardized mean difference would be calculated during the meta-analysis. Eliminating these data would greatly reduce the robustness of the results, therefore using *RII* as effect size seems a reasonable decision.

3.2. Abundance of ground beetles in edges

The distribution of ground beetle species at both the lower (herbivorous) and the higher (omnivorous, predatory) trophic levels changed significantly at the edges, as forest edges maintained by natural processes or by anthropogenic activities had significantly higher abundance than their interiors (Figs. 1–3). Nevertheless, in case of edges maintained by other anthropogenic activities (industry, recreation, or urbanization) the gradient of the sampling locations into the forest interior was incomplete (most interior sampling locations were at 100 m from the edge) to detect edge effect on the abundance of herbivore ground beetle species (Fig. 1). Similarly, up to 300 m from the edge, the abundance of predatory species was not significantly different between the forest edge and the interior in edges disturbed by forestry (Fig. 3).

3.3. Depth of edge influence

DEI on the abundance of ground beetle species at different trophic level was modulated by the edge maintaining processes (Table 1 and

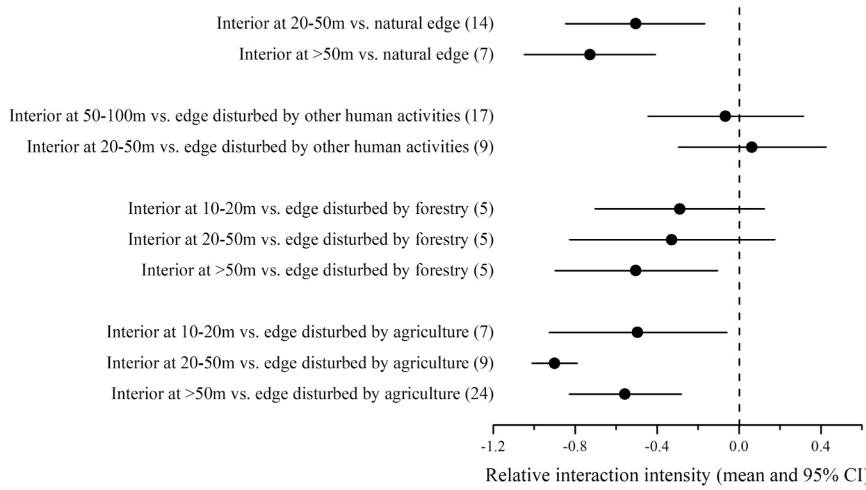

Fig. 1. Mean relative interaction intensity (RII) and the 95% bootstrapped confidence interval (with 999 iterations) showing the standardized difference between the mean abundances of herbivorous ground beetle species in the forest interior sites with different distance from edges and the forest edge sites. Values in brackets show the number of interior-edge comparisons for which the mean relative interaction intensity was calculated. Mean RII was only calculated for edge-to-interior comparisons of abundance data with ≥4 cases. A negative RII value indicates higher abundance in forest edges than interiors. Mean RII is statistically significant when the confidence interval does not include zero. The depth of edge influence (DEI) was defined as the distance over which there was no significant difference between the mean abundances at the forest edge and the interior.

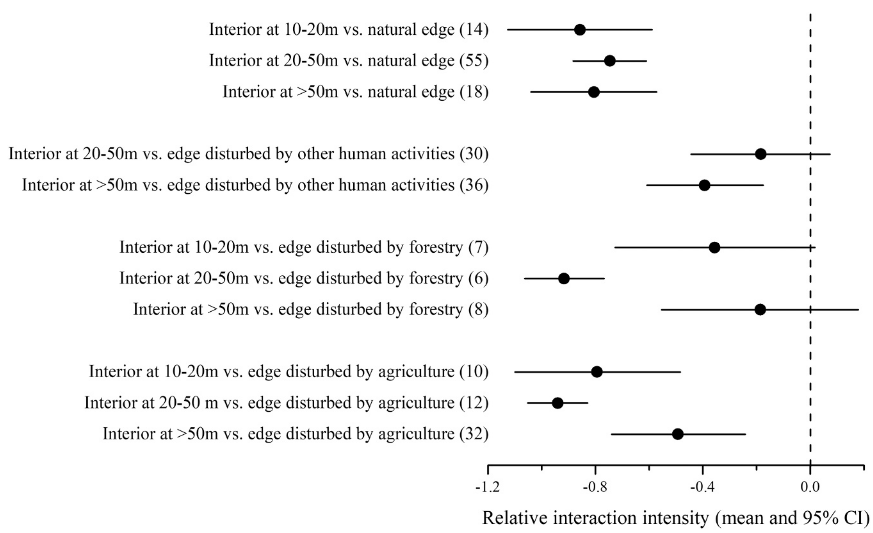

Fig. 2. Mean relative interaction intensity (RII) and the 95% bootstrapped confidence interval (with 999 iterations) showing the standardized difference between the mean abundances of omnivorous ground beetle species in the forest interior sites with different distance from edges and the forest edge sites. Values in brackets show the number of interior-edge comparisons for which the mean relative interaction intensity was calculated. Mean RII was only calculated for edge-to-interior comparisons of abundance data with ≥4 cases. A negative RII value indicates higher abundance in forest edges than interiors. Mean RII is statistically significant when the confidence interval does not include zero. The depth of edge influence (DEI) was defined as the distance over which there was no significant difference between the mean abundances at the forest edge and the interior.

Figs. 1–3). DEI on herbivore abundance was similar in natural and agriculture-influenced edges (< 20 m and < 10 m, respectively), while the edge effect penetrated deeper into the forest interiors under forestry (up to 50 m) or other anthropogenic activities (up to 100 m; Table 1 and Fig. 1). Similarly, omnivore abundance was similar in edges maintained by natural processes and agriculture (< 10 m), while greater in edges maintained by forestry or other anthropogenic activities (≤ 20 m and ≤ 50 m, respectively; Table 1 and Fig. 2). Surprisingly, at the interiormost sites (> 50 m from the edge) with forestry-generated edges, an additional edge effect on abundance of omnivores occurred (Fig. 2). DEI on the abundance of predatory species was similarly low with natural edges and agriculture-maintained edges (≤ 10 m and ≤ 20 m, respectively), while it was much higher in edges under the influence of forestry or other anthropogenic interventions (≤ 300 m and ≤ 50 m, respectively; Table 1 and Fig. 3).

In cases where the edge effect was identified (i.e. the mean RII value and its confidence interval did not include zero, indicating significant difference), the vast majority of the differences in mean RII values between different locations in the forest interior were not significant (Figs. 1–3). The only exception was the abundance of omnivores between the middle-interior (20–50 m from the edge) and the interiormost sites (> 50 m from the edge) in agriculture-influenced edges. This pattern suggested that as the edge effect was no longer present in the forest interior, the abundance of ground beetles did not change significantly.

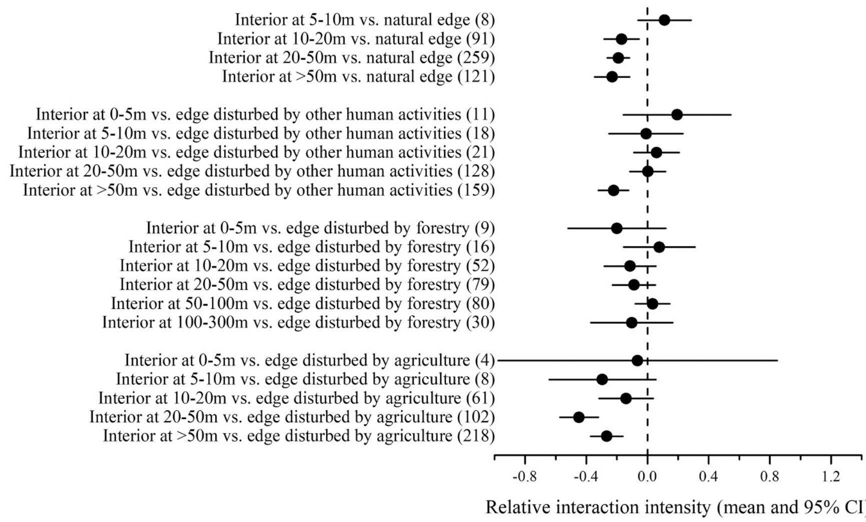

Fig. 3. Mean relative interaction intensity (RII) and the 95% bootstrapped confidence interval (with 999 iterations) showing the standardized difference between the mean abundances of predatory ground beetle species in the forest interior sites with different distance from edges and the forest edge sites. Values in brackets show the number of interior-edge comparisons for which the mean relative interaction intensity was calculated. Mean RII was only calculated for edge-to-interior comparisons of abundance data with ≥4 cases. A negative RII value indicates higher abundance in forest edges than interiors. Mean RII is statistically significant when the confidence interval does not include zero. The depth of edge influence (DEI) was defined as the distance over which there was no significant difference between the mean abundances at the forest edge and the interior.

Table 1
Depth of edge influence characterised by the abundance of ground beetles of different trophic habits at forest edges maintained by natural processes or by anthropogenic activities.

Feeding category	Depth of edge influence at various edges			
	Natural	Anthropogenic		
		Agriculture	Forestry	Other
Herbivorous	< 20 m	< 10 m	≤ 50 m	≤ 100 m
Omnivorous	< 10 m	< 10 m	≤ 20 m	≤ 50 m
Predatory	≤ 10 m	≤ 20 m	≤ 300 m	≤ 50 m

4. Discussion

4.1. Depth of edge influence in various edges

Similarly to the results of our previous studies on community-level parameters (Magura et al., 2017), life-history (body size, wing morphology, diet; Magura and Lövei, 2020a,b; Magura et al., 2019), and ecological traits (habitat affinity; Magura et al., 2017), our present results show that edge maintaining-processes affected also the DEI. DEI, characterised by abundance was generally larger at edges maintained by anthropogenic activities (except agriculture) than natural ones. Our results indicate similar edge responses for herbivore, omnivore and predatory ground beetles, as DEI on their abundance was similarly low in natural and agriculture-influenced edges, while it penetrated deeper into the forest interiors under forestry or other anthropogenic activities. To our knowledge, DEI on species at different trophic levels has not yet been investigated. Thus, our study fills this gap and emphasizes the importance of trait-based approaches in edge research. Furthermore, we showed that the abundance of ground beetles in forest interiors did not follow the increasing/decreasing pattern with distance from edges as one would expect from the linear edge response model (Ewers and Didham, 2006). Actually, the abundance trend is best described by a logistic edge response model, similarly to the pattern observed for other beetle taxa (Ewers and Didham, 2006). Quantifying mean DEI of previous studies for edges maintained by natural vs. anthropogenic processes (Table S4), also reported a narrower edge influence on abiotic parameters for natural (mean DEI= 11.12 m) than anthropogenic edges (26.9–57.3 m). Similarly, the average edge influence on biotic parameters extended over smaller distances into the forests across natural edges (mean DEI: 29 m) than across edges maintained by anthropogenic activities (40.0–95.2 m, Table S4).

4.2. Drivers of different DEI in various edges

Forest edges maintained predominantly by natural processes have a stratified horizontal structure with spatially extended, gentle gradient toward both the forest interior (shrub and sapling zones) and the adjacent open habitat (perennial herb zone; Forman and Godron, 1986). Such edges moderate wind speeds reaching the forest interior, preventing changes in vegetation composition and structure by windthrow. Furthermore, it may also decrease solar radiation levels penetrating into the forest edge and interior, maintaining a natural, stable gradient in microclimatic conditions (Hanson and Stuart, 2005). Previously it was stressed that structural characteristics of the forest edge can be a key driver of DEI on microclimatic, and consequently, on biotic parameters (Didham and Lawton, 1999), as increased cover and stratified structure of vegetation may reduce DEI by acting as an impermeable filter for dispersal of edge specialists and matrix species (Cadenasso and Pickett, 2001; Hanson and Stuart, 2005; Williams-Linera, 1990).

In contrast, anthropogenic forest edges are occasionally influenced by direct interventions and/or indirect (chemical and fertilizer drift) disturbances (Boutin and Jobin, 1998; Harper et al., 2005), leading to abrupt edges with little horizontally stratified vegetation and suddenly changing microclimatic conditions (Bergès et al., 2013). These abrupt edges are exposed to windthrow, leading to deep wind and light penetration and, resulting in high DEI in microclimatic parameters (Chen et al., 1995; Didham and Lawton, 1999). Such increased microclimatic DEI implicitly enhances DEI for biotic parameters, too.

The DEI differences demonstrated for ground beetles may exist for other organisms with a different trophic position. For example, different DEI across natural edges versus edges created by logging/thinning exists for plants (Cadenasso and Pickett, 2001, 2000; Hanson and Stuart, 2005).

4.3. Different DEI at anthropogenic edges

We found that DEI on the abundance of ground beetles generally extended over greater distances into the forests across edges occasionally disturbed by forestry (≤ 20–300 m) or other anthropogenic interventions (≤ 50–100 m) than across edges disturbed by agriculture (≤ 10–20 m). Previous studies on ground beetles quantifying the DEI across agricultural edges reported similar values (Bedford and Usher, 1994; Roume et al., 2011a). One possible explanation for the low DEI on abundance of ground beetles in edges maintained by agriculture is that the majority of the publications used in our meta-analysis (9 out of 14) studied intensively grazed, mowed grasslands, meadows, lawns, and sites in early stage of secondary succession, out of intensive production (fallows, set-asides) rather than classical arable fields. In the adjacent forest edges of these habitats the gradual, stratified horizontal vegetation structure may be just moderately impacted, allowing the maintenance of the microclimatic gradient and stratified vegetation structure, reducing the DEI (Cadenasso and Pickett, 2001; Hanson and Stuart, 2005; Williams-Linera, 1990). Another, more likely reason for short-range DEI in agricultural edges could be that individuals, dispersing from agricultural fields to aestivate, reproduce or overwinter in forest edges rarely penetrate deeply into the forest (Knapp et al., 2019; Roume et al., 2011b; Sklodowski, 1999).

Across edges disturbed by forestry or other anthropogenic interventions, DEI, reflected by ground beetle abundance was many times (even by one order of magnitude) larger than across edges with neighbouring cultivated fields. In edges still under forestry or other anthropogenic influences, due to repeated disturbances and less edge contrast than agricultural edges, DEI measured by microclimatic parameters extends deeper into the forest, making environmental conditions in interior similar to those at edges (Chen et al., 1995; Didham and Lawton, 1999). Previous studies on ground beetles also showed that carabid abundance was affected by edges under forestry influences even as far as 1000 m into the interior (Ewers and Didham, 2008; Henríquez et al., 2009; Lemieux and Lindgren, 2004; Pawson et al., 2011; Pearce et al., 2005).

4.4. *Consequences of long-range DEI*

Large-scale edge effects can lead to extreme reductions in population size or even to local extinction of forest specialist species that are restricted to habitat cores (Ewers and Didham, 2008). For the protection of forest-interior species at the landscape scale, knowledge on the size of habitat core areas is a central issue (Drake et al., 2002; Fahrig, 2003) and highly needed for conservationists to manage insular landscapes (Gascon et al., 2000; Wei and Hoganson, 2005). Wide DEI (up to 300 m) across edges created by forestry suggested by our analysis implies that forest fragments, assuming circular shape, would have to be at least ~ 330 ha in area to maintain at least half of their area as core habitat for forest-interior communities. However, forest fragments are rarely circular, so the necessary area may be even larger, and future climate warming can only exacerbate this edge effect.

The fact that DEI can extend up to 300 m into the forested habitat in case of edges created by forestry operations, also have important forest management implications. Nowadays, removing groups of trees and creating gaps is a widespread uneven-aged management method. Forest edges, however, are also formed during gap creation, potentially affecting adjacent unlogged forest stands by altering solar radiation and microclimate and by exposing trees to windthrows and crown diebacks (Matlack, 1994; Murcia, 1995). Understanding the spatial extent by which edge effects reduce the core area of unlogged forest stands is essential. Based on our results, we recommend that the shortest distance between gaps created by group selection should exceed 600 m. This would ensure that the unlogged forest stands between the gaps do not become edge habitats and can maintain intact forest-interior communities.

5. Conclusions

Using trophic position, one of the most important species traits related to edge responses, we showed that edge maintaining-processes uniformly affected DEI (characterised by abundance) on ground beetles, as DEI generally extended over greater distances into the forests across anthropogenic than natural edges. However, we also found differences in DEI at different anthropogenic edges. DEI across natural, gradual edges and edges with slightly preserved horizontally stratified vegetation structure (studied agriculture-modified edges next to intensively grazed, mowed grasslands, meadows, lawns, fallows, set-asides) were similar. In contrast, DEI across abrupt edges created by forestry or other anthropogenic interventions extended up to > 300 m into the forests, much deeper than across natural edges. We suggest that in order to maintain at least half of the original forest area as core habitat for forest-interior species and to preserve biodiversity and ecosystem functions and services, a fragment needs to be ~ 330 ha, and to create uneven-aged forest by gap-cutting while maintaining forest-interior species, the shortest distance between gaps should exceed 600 m.

CRediT authorship contribution statement

Tibor Magura: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Gabor L. Lövei:** Writing – review & editing, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121874.

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