



Article

The Permeability of Natural versus Anthropogenic Forest Edges Modulates the Abundance of Ground Beetles of Different Dispersal Power and Habitat Affinity

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Abstract: Forest edges are formed by natural or anthropogenic processes and their maintaining processes cause fundamentally different edge responses. We evaluated the published evidence on the effect of various edges on the abundance of ground beetles of different habitat affinity and dispersal power. Our results, based on 23 publications and 86 species, showed that natural forest edges were impenetrable for open-habitat species with high dispersal power, preventing their influx into the forest interiors, while forest specialist species of limited dispersal power penetrated and reached abundances comparable to those in forest interiors. Anthropogenic edges, maintained by continued disturbance were permeable by macropterous open-habitat species, allowing them to invade the forest interiors, while such edges (except the forestry-induced ones) deterred brachypterous forest specialists. Different permeability of forest edges with various maintaining processes can affect ecosystem functions and services, therefore the preservation and restoration of natural forest edges are key issues in both forest ecology and nature conservation.

Keywords: anthropogenic edges; dispersal; edge effect; filter function; forest interior; forest specialist species; invasion; open-habitat species; natural edges; spillover

1. Introduction

With the ongoing, world-wide habitat conversion, previously continuous habitats become fragmented, and the presence of edges becomes more and more prevalent in landscapes [1]. Edges are transitional zones between different habitats that occur naturally, and have substantial influence on abiotic and biotic landscape conditions [2].

The boundary zone between adjacent habitats often display attributes that are distinct from either its adjacent habitat [3,4]. These special conditions create habitat for edge-inhabiting species with highly dynamic abundance and flow-on changes in their biotic interactions from predation to seed dispersal at these edges [3]. With edges becoming ubiquitous, they are one of the most studied entities in ecology [1].

Edge research, through examining manifold species and diverse types of edges has given us an articulate picture of the edge effects [5]. Four fundamental phenomena were identified to account for changes in species abundance across habitat edges: ecological flows, access to spatially separated resources, resource tracking and species interactions [5]. A predictive model, driven by resource distribution, aimed to forecast changes in abundance near edges for any species in any landscape [6]. Although several responses are indeed predictable, several unexplained responses

limit the predictive power of this theory [6]. Edge orientation (edge position relative to the sun [5]), size and isolation of habitat patches, the quality of adjacent habitats, landscape composition [7], edge contrast (low vs. high [5,8]), the contrast between habitat patch and matrix [4], species traits (including habitat specialization, dispersal power, seasonal and diurnal activity, body size, reproduction [8,9], habitat suitability [8] and temporal effects from time of day to year [5]) can be responsible for the unexplained variation.

The edge-maintaining processes are also important drivers of the edge effect [10]. Magura et al.'s [11] “history-based edge effect hypothesis”, assumes that natural vs. continued human influence via forestry, agriculture, or urbanization will impact the diversity of edge-associated assemblages. Ground beetles in forest edges maintained by natural processes are significantly more species rich than those in their interiors, while such difference does not exist at edges with continued human influence [11]. Species richness, however, could be an imperfect indicator of the edge effect, because of species-specific responses to the same stimuli [12–14]. Therefore, taking into account species traits during analysis could provide a deeper understanding. Here we evaluated the edge effect considering dispersal power (a life history trait) and habitat affinity (an ecological trait) of ground beetles at forest edges. These traits were selected because dispersal power is closely related to population turnover [15] affecting assemblage stability, while the selected, widely different habitat preferences are expected to generate deviations in response to habitat fragmentation [11]. Our hypotheses were: (1) for open-habitat ground beetle species of high dispersal power, forest edges maintained by natural processes constitute a barrier and prevent their influx into the forest interior, while (2) edges under continued human influences are penetrable; (3) for forest specialist carabids of limited dispersal power, edges maintained by natural processes are penetrable, while (4) edges with continued human influences are not. To test these hypotheses, we evaluated published evidence to compare the abundance of these groups at edges vs. interiors.

In the present study, we found support for all four hypotheses: different permeability of forest edges with various maintaining processes fundamentally determined the spatial dispersal of ground beetles with different dispersal power and habitat affinity.

2. Materials and Methods

2.1. Data Search and Selection

We searched the literature for relevant data on 27 May 2016 at the University of Debrecen, Hungary using the Web of Science platform with the “All databases” option. The following search string was used: TOPIC = (forest*) AND TOPIC = (edge* OR margin*) AND TOPIC = (carabid*), with a time period limit of 1975–2015. We also reviewed the bibliography of the papers found by the search for additional, relevant publications that had remained undetected. Our inclusion criteria were: the paper had to report data on carabid abundance, variability and sample sizes, from both forest interior and forest edge. From papers that studied carabids along transects, only data from the interior most location in the forest were used.

We found 204 relevant publications, 199 from the search in Web of Science and five from the reference lists of these papers. Of these, 53 papers reported abundance data from both forest interior and forest edge. Mean abundance of ground beetle species (with standard deviations and sample sizes) for forest interiors and edges were extracted from 23 studies (Table S1). Twelve papers studied forest edges with continued human influences, and 11 papers that studied forest edges maintained by natural processes. Of the edges with human influence, 5 were created by agriculture, 4 by forestry, and 3 by urbanization. Out of the five papers dealing with edges disturbed by agriculture, only one studied grassland as adjacent habitat, while the other four had agricultural fields as neighboring habitats, therefore these edges were grouped to “edges disturbed by agriculture”. The 23 papers reported abundance data on 35 open-habitat species that were good dispersers (“flying grasslanders”) and 51 poor disperser forest specialists (“walking specialists”; Table S2). Overall, our meta-analyses were

based on 200 discrete edge-to-interior comparisons of abundance data concerning 86 ground beetle species (56 comparisons for open-habitat species and 144 ones for forest specialist species).

2.2. Classification of Edges Based on Their Maintaining Process

We classified forest edges according to their maintaining processes. In order to be classified as maintained by natural processes (succession), neighboring habitats (the forest interior and the adjacent grassland or meadows) had to be unmanaged (without cutting, thinning, intensive grazing, mowing or fire damage) for at least 50 years. Disturbance-maintained edges included those created by forestry (clear-cutting, or forest management operations), urbanization (forest patches embedded in, and adjacent to an urbanized area) or agriculture (the habitat neighboring the forest edge was cultivated, intensively grazed, mowed and/or regularly burned). We excluded edges where there was a mixture of various forces, and also those with shifts between natural and human influence over time.

2.3. Data Analyses

Ground beetles were categorized according to their dispersal power and habitat affinity. Short-winged (brachypterous) species were considered poor dispersers, while macropterous species were classified as good dispersers. Species associated with open-habitat were considered open-habitat species, while species restricted to forests were classified forest specialists. This categorization was made using information in the original papers; when this information was lacking, we consulted an online ground beetle database [16].

For each comparison, Hedge's unbiased standardized mean difference (Hedges' g) was calculated as:

$$g = J \frac{\overline{X}_F - \overline{X}_E}{S_{within}}, \quad (1)$$

$$S_{within} = \sqrt{\frac{(n_F - 1)S_F^2 + (n_E - 1)S_E^2}{n_F + n_E - 2}} \quad (2)$$

and

$$J = 1 - \frac{3}{4(n_F + n_E - 2) - 1} \quad (3)$$

where \overline{X}_F and \overline{X}_E denote the mean abundance of beetles in forest interior and forest edge, respectively, n_F and n_E are the sample sizes at the forest interior and forest edge, and S_F and S_E are their respective SDs. A negative g value indicates higher beetle abundance in forest edges than interiors, while a positive one shows higher abundance in forest interiors compared to forest edges.

Subgroup meta-analysis was used to examine whether the forest edge maintenance class (natural or anthropogenic) had an effect on ground beetle abundance. The overall effect and the effects of moderators (type of edge-maintaining process; type of human influence) were examined by random-effects models because of differences in geography, experimental conditions, design and research methods. One publication could provide data for several edge-to-interior abundance comparisons, thus we included a publication-level random effect as a nesting factor into the model. The mean effect size was considered statistically significant when the 95% bootstrap confidence interval (calculated from 999 iterations) did not include zero.

To describe heterogeneity, complementary measures of Q and I^2 were calculated [17]. Total variance (Q_{total}) was partitioned into within- (Q_{within}) and between group ($Q_{between}$) components and were tested for statistical significance [17]. Significant variance between groups ($Q_{between}$) means that edge effect on abundance significantly differed according to the edge-maintaining processes. During the calculations, only datasets with at least five edge-to-interior comparisons of abundance data from at least three different papers were included to keep statistical power. Publication bias was tested using funnel plots and the Egger test [17]. In case of significant asymmetry, the trim and fill method was

employed [18]. Calculations were performed using the *MAd* (version 0.8-2 [19]) and *metafor* packages (version 1.9-9 [20]) in R programming environment (version 3.6.3 [21]).

3. Results

Considering all edges, the abundance of flying grasslanders (good disperser open-habitat species) was significantly higher in the edges than the interior (Figure 1a). Abundance pattern, however, was different according to the history of edges, although the between group variance ($Q_{between}$) was not significant (Table S3). At edges maintained by natural processes, the abundance of flying grasslanders was higher than those in the respective forest interiors, while no similar pattern occurred in edges maintained by human influence. Similarly, edges created by forestry activities showed no such difference (Figure 1a, Table S3). Neither the total nor the unexplained heterogeneity was significant (Table S3), and no significant funnel plot asymmetry was detected by the Egger tests (weighted or mixed-effects meta-regression) (Table S4). Nevertheless, the trim and fill method estimated 12 missing abundance data on the right side of the funnel plot (Figure S1a). Adding these data, however, did not change the significance of the overall effect in the model (Table S5).

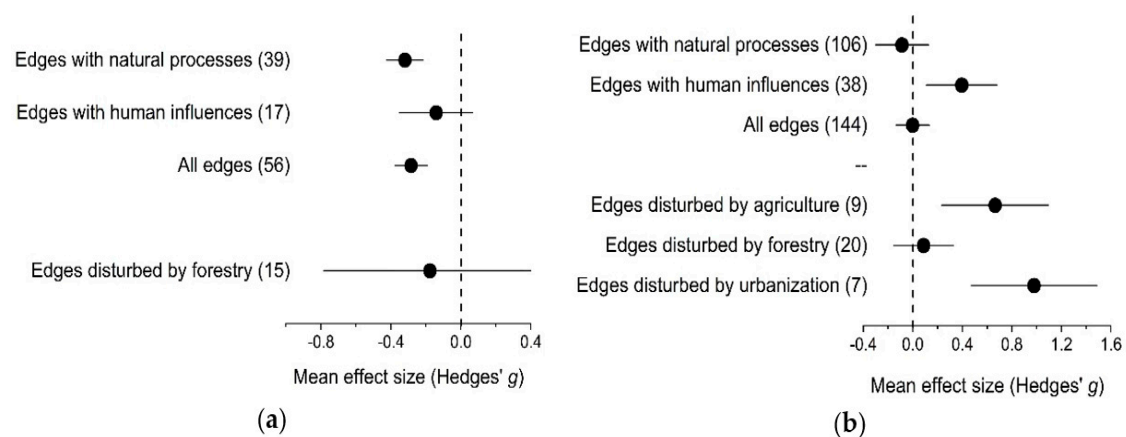


Figure 1. Mean effect sizes of random-effect models ($\pm 95\%$ confidence interval) for the abundance of flying grasslander (good disperser open-habitat) (a), and walking specialist (poor disperser forest specialist) ground beetle species (b). Values in brackets show the number of abundance values for which the mean effect size was calculated. Mean effect size was only calculated for edge-to-interior comparisons of abundance data with ≥ 5 cases. A negative g value indicates higher abundance in forest edges than interiors. Mean effect size is statistically significant when the confidence interval did not include zero.

Analyzing all edges together, there was no significant difference in the abundance of walking specialists (poor disperser forest specialists) between forest edges and their interiors (Figure 1b). The trends, however, was significantly different according to the maintaining forces (significant $Q_{between}$, Table S3). At edges with natural processes, the abundance of walking specialists was similar in edges and interiors, while in the case of edges with human influences, there were significantly fewer individuals there than in the forest interiors. Furthermore, the edge effect on the abundance of walking specialists was also significantly related to the type of human disturbance (significant $Q_{between}$, Table S3). In edges disturbed by agriculture or urbanization, the abundance at edges was significantly lower than in interiors, while there was no such difference at forestry-influenced edges (Figure 1b, Table S3). The total and the unexplained heterogeneities were significant in all models except in the case of agriculture-generated edges (Table S3). The Egger tests indicated significant funnel plot asymmetry (Table S4). The trim and fill method also estimated 7 missing abundance data on the left side (Figure S1b), but adding these did not change the non-significance of the overall effect (Table S5).

4. Discussion

The history-based edge effect hypothesis [11] assumes that different edge-maintaining processes (natural vs. continued human influence) have significant impacts on the spatio-temporal distribution of species across edges and the diversity of assemblages in edges and adjacent habitats. Indeed, ground beetle species richness was significantly higher in forest edges maintained by natural processes than the forest interiors, while there was no similar difference between edges with continued human influences and their respective forest interiors [11]. Species richness or taxonomic diversity, however, is not necessarily the most useful indicator to identify edge effects because species with various traits (in size, dispersal power, feeding habits, tolerance limits) may trigger different responses to changes in abiotic and biotic factors along edges [12–15]. Therefore, to reveal real ecological patterns, species with different traits should be analyzed separately to assess their responses to edge effects at both species and assemblage levels [22,23].

To date, the history-based edge effect hypothesis was scrutinized using body size [24], feeding habit [25], and habitat affinity [11] across variously maintained forest edges. The abundance of small-sized species was significantly higher at edges maintained by natural processes than in their interior, but no such difference was found in the case of forest edges maintained by agriculture or forestry. Furthermore, there is no significant difference in the abundance of either the medium-sized or the large-sized species between any type of forest edge and its interior [24]. Regarding feeding habits, the abundance of herbivorous, omnivorous, and predatory ground beetle species is significantly higher at edges with natural processes than their interiors, while no similar pattern occurs in edges with continued human influences [25]. The abundance of forest specialist species is not significantly different at edges maintained by natural processes with respect to their interiors. However, forest specialists avoid edges disturbed by agriculture or urbanization, while there is no such reaction to forestry-influenced edges [11]. Both the generalist and the open-habitat species are significantly more abundant in the edges than in interiors, irrespective of the kind of edge encountered. This difference is not registered when the edge was forestry-influenced [11].

Our study, combining a life history (wing morphology) and an ecological trait (habitat affinity), shows that the abundance of open-habitat species, which are good dispersers, was significantly higher in the edges maintained by natural processes compared to their interiors, while anthropogenic interventions, mainly forestry makes the edge penetrable, and their abundance becomes more even. Contrary to this, the forest specialist species, which are poor dispersers, approached and entered forest edges with natural processes and reached abundances similar to interiors, but they avoided edges influenced by agriculture or urbanization, although not forestry-disturbed edges. In accordance with previous results based on only a single ecological trait (habitat affinity), it seems that the filter function of edges is fundamentally different depending on their maintaining processes, that is, on their history [11]. For flying grasslander species inhabiting the surrounding open-habitats, edges with human influences, mainly by forestry activities, were penetrable, and these species also invaded the forest interior. However, naturally maintained forest edges, became impenetrable barriers, preventing the influx of these species into the forest interior. For walking specialist species, edges maintained by natural processes are penetrable, allowing them to disperse from forest interiors to edges, to move right even through the edges into the adjacent habitats [14]. Forestry-influenced edges seems to have filter function similar to edges with natural processes. However, edges maintained by agriculture or urbanization seemed impenetrable, preventing the dispersal of walking specialists into the edges, and thus limiting their possibility to disperse beyond the forest fragment. Different filtering function of forest edges with various maintaining processes was confirmed not only for ground beetles but also for other organisms and habitat parameters. Evaluating vegetation responses at boreal forest edges with various history, Harper et al. [26] also showed notable differences between forest structure responses to natural (fire) and anthropogenic (cut) edge influences.

Graduality (or abruptness) and permanence could be the main causes of the different filter function of variously maintained forest edges [26,27]. Natural processes (succession after natural disturbances,

such as fire, insect outbreaks, windthrow, grazing and habitat disturbance by wildlife) create and maintain complex, heterogeneous, permanent, stratified, and gradual transitional zones extending up to 5–30 m outside the forest toward the adjacent habitat, and up to 10–30 m toward the interior of the forest [26,28–30]. These features of forest edges with natural processes constitute gradual changes in habitat structure and environmental conditions across the transitional zone. Permanent, successively changing structure and conditions, on the one hand, allow the spreading of walking specialist species from the forest interior to the edge, and provide an opportunity to disperse beyond the forest. On the other hand, these edges have a buffer function by preventing the influx of flying grasslander species into the forest interior [11]. Contrary to this, repeated anthropogenic disturbance (cultivation, intensive grazing, mowing, burning, forestry interventions, urban management operations) regularly destroys the development of complex, permanent, gradual edges, thus forming and maintaining a simplified, abrupt and often narrow transition zone. These characteristics of edges with human influences create abrupt changes in habitat structure and environmental parameters, limiting the permeability of these edges for forest specialist species, but from the other direction, allow the influx of open-habitat species into the forest interior [11].

The invasion of open-habitat species into the forest interiors may have harmful effects on the forest specialist species through biotic interactions, including resource competition and depletion, and even intraguild-predation [31]. Both intensive agriculture, forestry and progressive urbanization tend to eliminate natural, semi-natural habitat patches, including forest remnants, thus these human activities can be considered one of the greatest current threats to forest specialist species [32–38], impoverishing community composition and simplifying its organization [39,40], and damaging ecosystem functions and services [41,42]. The impoverishment and/or compositional changes of forest interior assemblages caused by the invasion of open-habitat species across edges with continued human influences, as well as the restricted dispersal or spillover of forest specialist species into these edges and the adjacent fields may have negative effects on ecosystem functions and services, like biological pest control, and decomposition [25]. Indeed, a recent study indicated limited predator spillover from native forest fragments across edges disturbed by agriculture to maize fields in central Argentina [43].

Our results also underline that forestry-induced edges are penetrable for walking specialist species, allowing them to disperse from forest interiors to edges. This result seems surprising, as it was shown that changes in habitat structure and environmental conditions in forest edges under forestry influences are detrimental for biodiversity [3]. Forestry-induced edges are mainly created by timber harvesting and the harvested sites will usually be reforested. Regeneration of these sites can reduce the contrast between the neighboring habitats, softening the edge effects [44]. Studying the edge influence on forest and understory structure and composition at forest edges adjacent to regenerating clear-cut originated sites, it was shown that significant edge effects are of relatively short duration [45]. In the first two years after harvesting, significant responses were detected to edge creation, but the edge influence weakens with time. This weakening of the edge influence resulted from the re-establishment of edge-related microclimatic gradients due to rapid regeneration of the adjacent, harvested habitat [45]. In forestry-generated edges, the regeneration of edge gradients in habitat structure and environmental conditions allow forest species to disperse into such edges. Moreover, this dispersion is strongly facilitated by the recovery potential of forest ground beetles after the canopy closure (8–16 years after the reforestation) in regenerating habitats [46–48].

Significant total and unexplained heterogeneity in the models concerning walking specialist species suggests that in addition to the history of forest edges, other features may be important in determining the spatial distribution of these species across edges. The size, isolation and quality of the neighboring habitats, the temporal effects and edge orientation are among important factors [5]. Moreover, other traits of the forest specialist species (body size, feeding habit, activity, and reproduction type) may also be responsible for the remaining heterogeneity, thus could be additional, important factors determining edge responses by these species. A global meta-analysis considering all the

above-factors would be challenging but very useful to further examine and articulate the history-based edge effect.

Our results highlight that different maintaining processes (natural vs. anthropogenic) fundamentally determined the permeability of forest edges, the spatial dispersal of flying grasslander species and walking forest specialist ground beetle species across edges. This difference can basically affect both the biodiversity in edges and the local ecosystem functions and services. Therefore, all edges maintained by natural processes should be preserved and unfavorable changes to their structure and characteristics should be avoided to ensure their proper functioning. Simultaneously, if possible, human-induced edges should be restored (e.g., by softening these edges [44]) to develop a filter function similar to edges with natural processes.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/12/9/320/s1>, Figure S1: Funnel plots with missing data (empty circles) for the abundance of flying grasslander (macropterous open-habitat) (a) and walking specialist (brachypterous forest specialist) ground beetle species (b), Table S1: Studies used in the meta-analyses, Table S2: Ground beetle species included into the meta-analyses, their dispersal power and habitat affinity, and the papers from which their abundances were extracted, Table S3: Estimates and heterogeneities in the models, Table S4: Results of regression test for funnel plot asymmetry of abundances of flying grasslander (macropterous open-habitat) and walking specialist (brachypterous forest specialist) ground beetle species, Table S5: Model results after trim and fill for the abundances of flying grasslander (macropterous open-habitat) and walking specialist (brachypterous forest specialist) ground beetle species.

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