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THE TYPE OF FOREST EDGE GOVERNS THE SPATIAL DISTRIBUTION OF DIFFERENT-SIZED GROUND BEETLES

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Worldwide human-induced habitat fragmentation intensifies the emergence of forest edges. In addition to these edges, there are edges evolved by natural processes. Edge-maintaining processes (natural vs. anthropogenic) fundamentally determine edge responses, and thus edge functions. Species with various traits show fundamentally different edge response, therefore the trait-based approach is essential in edge studies. We evaluated the edge effect on the body size of ground beetles in forest edges with various maintaining processes. Our results, based on 30 published papers and 221 species, showed that natural forest edges were impenetrable for small species, preventing their dispersal into the forest interiors, while both the medium and the large species penetrated across these edges and dispersed into the forest interiors. Anthropogenic edges maintained by continued human disturbance (agriculture, forestry, urbanisation) were permeable for ground beetles of all size, allowing them to invade the forest interiors. Overwintering type (overwintering as adults or as larvae) was associated with body size, since almost two-thirds of the small species, while slightly more than a third of both the medium and the large species were adult overwintering. Based on this, size-dependent permeability of natural edges may be related to overwintering type, which basically determines species tolerance to human disturbance.

Keywords: spatial distribution, ground beetles, body size, carabids, edge effect, filter function, meta-analysis.

INTRODUCTION

Over the 20th century, the focus of ecological research gradually shifted from the study of undisturbed ecosystems to disturbed or human-managed ones. This trend reflects the continued increase in habitat conversion, in parallel with the globally increasing resource use by the human population. ‘Natural’ habitats, however, are not only shrinking but are also undergoing fragmentation, which inevitably creates more and more edges. Habitat edge is a type of ecotone, a transitional zone between adjacent ecological systems, with characteristics defined by space, time and the strength of interactions between the adjacent ecological systems (Turner & Gardner 2015).

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Habitat edge is defined at the meso-spatial scale and community level. At the border between two neighbouring habitats, environmental parameters are gradually or abruptly altered, creating conditions that are considerably different from either of the adjacent habitats (Murcia 1995, Ewers & Didham 2006). These conditions have a direct impact on the spatio-temporal distribution and dynamics of many species as well as their interactions. The totality of these is termed the "edge effect" (Murcia 1995).

Accumulated research on a wide range of organisms and diverse edge types has led to attempts to identify overarching mechanisms causing edge effects. Ries *et al.* (2004) suggested four such mechanisms: ecological flows, access to spatially separated resources, resource mapping, and species interactions. Ries and Sisk (2004) presented a predictive model forecasting abundance changes near edges for any species in any landscape, and this can predict several but not all edge responses. Edge orientation (Ries *et al.* 2004), temporal effects (Ries *et al.* 2004), habitat fragmentation (Ries *et al.* 2004, Hardt *et al.* 2013), edge contrast (Ries *et al.* 2004, Peyras *et al.* 2013), the difference between habitat patch and matrix (Ewers & Didham 2006), species traits (Peyras *et al.* 2013, Carvajal-Cogollo & Urbina-Cardona 2015) and habitat suitability (Peyras *et al.* 2013) were claimed to account for the unexplained variation.

Processes maintaining habitat edges also influence the edge effect (Strayer *et al.* 2003). A meta-analysis, focusing on forest edges, and on an abundant insect group, ground beetles (Coleoptera: Carabidae) shows that forest edges maintained by natural processes have significantly higher species richness than forest interiors, unlike edges under continued anthropogenic influence (history-based edge effect hypothesis, Magura *et al.* 2017). Species richness, however, is not the most sensitive indicator of the edge effect, because species with different traits may respond differently to the same stimuli (Koivula *et al.* 2004, Gobbi & Fontaneto 2008, Brigić *et al.* 2014, Magura 2017). A trait-based analysis could unearth otherwise hidden but important ecological patterns (Nagy *et al.* 2018), and neglecting the biology of organisms may derail attempts to understand their ecological responses (Lövei & Magura 2006).

Body size is an essential and widely used proxy for various life-history parameters (Peters 1983). Body size not only influences morphology, physiology and fitness of the organism (Kingsolver & Huey 2008), but is also linked to multiple life-history traits, including life span, fecundity, and behaviour (Chown & Gaston 2010), as well as to spatial distribution (Jetz *et al.* 2004, Davey *et al.* 2005) and biotic interactions, with consequences on community dynamics, and ecological networks (Woodward *et al.* 2005). Consequently, changes in body size distribution within assemblages have important consequences for ecosystem functioning (Petchey & Belgrano 2010, Ohlberger 2013).

To further articulate the history-based edge effect hypothesis, we compared the abundance of ground beetles of different body size (as a life history trait) classes captured at differently maintained forest edges and their respective interiors. We predicted that forest edges maintained by natural processes have significantly more large but not medium-sized or small ground beetles than their interiors, while edges with continued anthropogenic influence did not show such a trend.

MATERIAL AND METHODS

Study and data selection

To collect relevant data, we followed the procedure described in Magura *et al.* (2017). We used the resulting dataset with the same inclusion criteria: a paper had to report data on the abundance of the same carabid species in both forest interior and its respective edge. From papers that studied carabids along transects, only data from the two extremes: the interiormost location and the edge were used.

Classification of forest edges

Forest edges were classified as either maintained by natural processes, or by human interventions/disturbance. When neither of the neighbouring habitats have been managed (e.g. intensive grazing) or disturbed (by e.g. fire) for >50 years, we considered the edge a "natural" one. Edges created by human intervention (forestry, urbanisation or agricultural cultivation), and where the above non-disturbance criteria did not hold, were considered to be maintained by disturbance. The particular type of ongoing human intervention was a secondary classification criterion.

Data analyses

The body size of beetles was characterised by body length (Chown & Gaston 2010) and we classified carabids as small (geometric mean < 10.5 mm), medium (10.5–15 mm) or large (>15 mm). We calculated geometric means (as suggested by Chown & Gaston 2010) from minimum and maximum body length values obtained from Homburg *et al.* (2014). Subsequently, all analyses were based on this classification (Elek & Lövei 2007, Bell *et al.* 2017, Kędzior *et al.* 2020).

For statistical analyses, we calculated the unbiased standardised mean difference (Hedges' g) as a common effect size (Borenstein *et al.* 2009) as described in Magura *et al.* (2017). Subgroup meta-analysis considering the edge-maintaining forces as moderators (type of edge maintaining process; type of anthropogenic influence) was applied using a random-effects model with publication-level random factor. Heterogeneity in the data was tested by calculating Q and I^2 values (Borenstein *et al.* 2009). We partitioned total variance (Q_{total}) into within- (Q_{within}) and between group ($Q_{between}$) variances and tested them separately (Borenstein *et al.* 2009). Calculations were done using the MAd (DelRe & Hoyt 2014) and metafor packages (Viechtbauer 2010) in the R programming environment (R Core Team 2017). For further details, refer to Magura *et al.* (2017).

RESULTS

During the literature search, 204 published papers were found. Only 53 papers contained species abundance data from both the forest interior and the forest edge. Of these papers, however, only 30 studies reported standard deviations and sample sizes for the mean abundance values (Appendix, Table S1). Eleven papers studied forest edges maintained by natural processes, while 19 papers forest edges under continued human influences. One paper studied simultaneously two types of anthropogenic edges. Of the 20 edges with human influences, 8 were created and maintained by agriculture, 9 by forestry, and 3 by urbanisation. The 30 papers reported abundance data from 221 ground beetle species, of which 74 were small, 52 medium, and 95 large species. Overall, our meta-analyses were based on 466 separate edge-to-interior comparisons of abundance data of these 221 ground beetle species (Appendix, Table S2).

Analysing all edges together, the abundance of small species was significantly higher in the edges than in the interior (Fig. 1a; Appendix, Table S3). A similar pattern occurred in both the edges maintained by natural processes and the edges with continued anthropogenic influence. However, analysing separately the types of anthropogenic edges, no such pattern was observed. The abundance of small species was similar in forest edges maintained by agriculture or forestry and the respective forest interiors (Fig. 1a; Appendix, Table S3). Except for the models on natural edges and edges disturbed by agriculture, both the total and the unexplained heterogeneities were significant (Appendix, Table S3). Egger tests indicated significant funnel plot asymmetry (Appendix, Table S4). The trim and fill method estimated 24 missing abundance data on the right side (Appendix, Fig. S1a), but adding these did not change the significance of the overall effect in the model (Appendix, Table S5).

Considering all edges together, there was no significant difference in the abundance of medium species between forest edges and their interiors (Fig. 1b; Appendix, Table S3). The same lack of significant difference was observed for both natural and human-disturbed edges (Fig. 1b; Appendix, Table S3). Except for the model on edges disturbed by agriculture, both the total and the unexplained heterogeneities were significant (Appendix, Table S3) but without significant funnel plot asymmetry (Appendix, Table S4). The trim and fill method estimated 13 missing abundance data on the right side of the funnel plot (Appendix, Fig. S1b). Adding these data, however, did not change the non-significance of the overall effect (Appendix, Table S5).

The abundance of large species was, however, significantly higher in the edges than in the interior (Fig. 1c; Appendix, Table S3). This significant difference, however, disappeared when edges with different maintaining forces were analysed separately (Fig. 1c; Appendix, Table S3). Both the total and the unexplained heterogeneities were significant (Appendix, Table S3), with significant funnel plot asymmetry (Appendix, Table S4). The trim and fill method, however, predicted no missing abundance data (Appendix, Fig. S1c), so the significant overall effect in the model did not change (Appendix, Table S5).

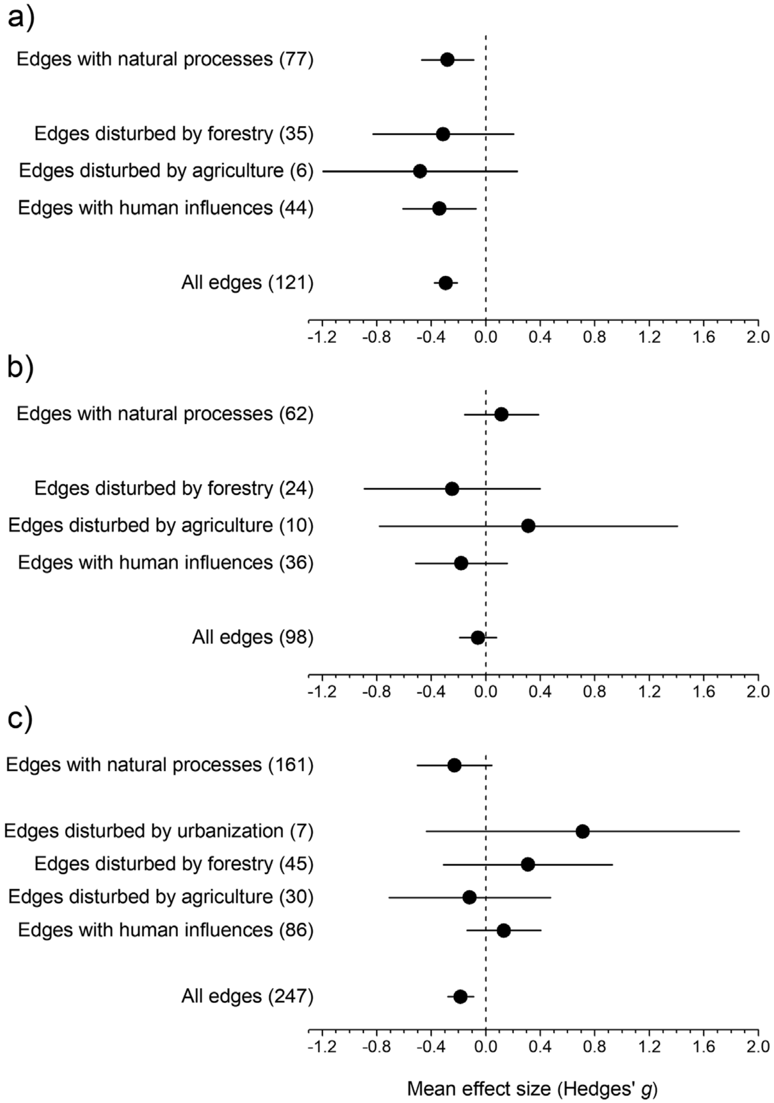

Fig. 1. Mean effect sizes of random-effect models (±95% confidence interval) for the abundance of small (a), medium (b) and large ground beetle species (c). Values in brackets show the number of species abundances for which the mean effect size was calculated. A negative *g* value indicates higher abundance in forest edges than interiors. The mean effect size is statistically significant when the confidence interval does not include zero

DISCUSSION

Our results, studying the spatial distribution of 221 ground beetle species with different body size across variously maintained forest edges from 30 studies, shows that the abundance of small species was significantly higher in the forest edges maintained by natural processes compared to their interiors, but not in edges maintained by agriculture or forestry. Previous studies on the spatial distribution of ground beetles across edges examined the abundance of species displaying different feeding habits (Magura *et al.* 2019), habitat affinity (Magura *et al.* 2017), and combined life history and ecological traits (dispersal power and habitat affinity, Magura & Lövei 2020*b*). The abundance of herbivorous, omnivorous, and predatory ground beetles were all significantly higher at edges with natural processes than their interiors, but no such difference was found in edges under continued human influence (Magura *et al.* 2019). Forest specialists were equally abundant at natural edges and their interiors, but they avoided edges disturbed by agriculture or urbanisation. The abundance of both the generalist and the open-habitat species were significantly higher at natural edges compared to the forest interiors, while these species reached similar abundance in the forestry-induced edges and the forest interiors (Magura *et al.* 2017). Open-habitat species with high dispersal power were significantly more abundant in natural edges than interiors, while became more similar in edges under anthropogenic interventions compared to their interiors. Contrary to this, the forest specialist species of limited dispersal power showed similar abundances in natural forest edges and interiors, but avoided edges influenced by agriculture or urbanisation (Magura & Lövei 2020*b*). In accordance with the history-based edge effect hypothesis (Magura *et al.* 2017), our results clearly demonstrate, that the permeability (the filter function) of edges is essentially different depending on their history (maintaining processes) (Strayer *et al.* 2003, Magura *et al.* 2017).

The history of edges may determine the structural and functional properties as well as ecological conditions at edges (Strayer *et al.* 2003, Harper *et al.* 2015). Permeability is one of the most critical functional features of forest edges, as it fundamentally determines the community composition and organisation in adjacent habitats (Lacasella *et al.* 2015, Boetzl *et al.* 2016, Knapp *et al.* 2019, Magura & Lövei 2019). Natural processes (succession after natural disturbances) maintain complex, stratified, heterogeneous, permanent, gradual forest edges extending up to several meters toward both the adjacent habitat and the forest interior (Magura 2002, Cadenasso *et al.* 2003, Harper *et al.* 2005, Harper *et al.* 2014). Contrary to this, repeated human disturbance (agriculture, forestry, urbanisation) prevents the development of permanent, complex, and gradual edges, thus allowing only to evolve a simplified, abrupt, and often narrow edges (Strayer *et al.* 2003, Harper *et al.* 2005, Turner & Gardner 2015). This difference in the graduality (or abruptness) and permanence between natural and anthropogenic forest edges could be the main cause of the different permeability and filter function of edges (Bowersox & Brown 2001, Strayer *et al.* 2003).

Our results show that anthropogenic forest edges allow small, medium, as well as large ground beetles to penetrate the forest interior. Natural forest edges also allow the dispersal of medium- and large species into the forest interior, but they prevent the influx of small species. Body size per se is a useful proxy, but cannot explain this size-dependent permeability of natural edges. Other life history and/or ecological traits associated with body size may underlie this pattern. For example, small carabids are usually macropterous or dimorphic, so they have high dispersal power (Kotze & O'Hara 2003, Jelaska & Durbešić 2009). Natural forest edges, being more dense, gradual and wider, can be impenetrable for species with high dispersal power. Indeed, most of the studied small species (54 out of 74 species; 73%) were macropterous or dimorphic. Similarly, 65% of the medium-sized species (34 out of 52 species) had also high dispersal power. However, only a small proportion of large species (24 out of 95 species; 25%) were macropterous or dimorphic. Thus, it is unlikely that this size-dependent permeability of natural edges was related to dispersal power, because roughly the same proportion of small and medium species had high dispersal power, yet their spatial pattern was fundamentally different across natural edges. An ecological characteristic that may also be associated with small body size is habitat affinity. Open-habitat and generalist species tend to have smaller bodies (Kotze & O'Hara 2003, Spake *et al.* 2016). Previously it was shown that natural forest edges were impermeable for both the open-habitat and generalist species (Magura *et al.* 2017). In the present situation, the proportion of open-habitat and generalist species was 77% for the small, 64% for the medium-sized, and 43% for the large species. The ratio of open-habitat and generalist species in the small and the medium-sized species groups was mostly similar, but their spatial pattern along natural edges was significantly different. Therefore, in the present study, different habitat affinity could not explain the size-dependent permeability of natural edges. Interactions between the above life history (wing form) and ecological trait (habitat affinity) can be a meaningful indicator (Magura & Lövei 2020*b*) to test the size-dependent permeability of natural edges. The proportion of macropterous or dimorphic matrix (open-habitat and generalist) species was 64% for the small, 48% for the medium-sized, and 20% for the large species. Thus, the combination of these traits again does not support the different spatial pattern of variously sized species across natural edges. Another key trait to explain our result of the size-dependent spatial pattern of ground beetles along forest edges maintained by natural processes may be the species tolerance to human disturbance. Persistence in a habitat generally depends on the most vulnerable life stage. The larval stage of ground beetle ontogeny is the most vulnerable life stage, as larvae have limited mobility, weak chitinisation, and therefore narrower tolerance limits than adults (Lövei & Sunderland 1996). Generally, two reproduction types of ground beetles can be distinguished, species with summer larvae (also called spring breeders; species overwintering as adults) versus species with winter larvae (autumn breeders; species overwintering as larvae). Species overwintering as adults (species with summer larvae) are usually abundant in disturbed habitats, suggesting their tolerance to disturbance regimes (Ribera *et al.* 2001, Magura *et al.* 2002). In our dataset, there was a remarkable difference in the proportion of disturbance tolerant species with summer larvae among the body size categories, since 65% of the small species, 39% of the medium, and 36% of the large species were adult overwintering. This pattern correlates well with the differences in the spatial pattern of differently sized species along natural forest edges. Based on this, it seems that natural forest edges do not allow disturbance tolerant small species with summer larvae, to penetrate the forest interiors. This could be explained by the fact that the environmental conditions (e.g. temperature, humidity, solar radiation, habitat structure) at the edge cannot extend deep into the forest interior (Strayer *et al.* 2003, Ries *et al.* 2004), thereby maintaining the strong environmental filter function of the stable, undisturbed forest interior (Magura & Lövei 2019). Strong environmental filter (e.g. high humidity, low temperature, thick leaf litter layer, closed canopy) in forest interior bordered by edges with natural processes prevent the survival and persistence of disturbance tolerant small species with summer larvae. Of course, in addition to the above mentioned, other traits (e.g. time of activity, hunting strategy, preference for environmental parameters) or their interactions may influence the spatial patterns of ground beetles across forest edges, as it was also indicated by the significant total and unexplained heterogeneity in the models. Moreover, other features of edges (type, size, age, and isolation of the neighbouring habitats, temporal effects and edge orientation), as well as the management type of the habitats adjacent to edges may also be important in determining the species pool and the spatial distribution of ground beetle species across edges (Blake *et al.* 1994, Holland 2002, Ries *et al.* 2004, De Smedt *et al.* 2019).

Our results show that ground beetle species in each size category were abundant in all edges. From the edges, beetles can easily disperse out of the forest, delivering insect pest and weed control in the adjacent habitats, especially in neighbouring agricultural fields (Roume *et al.* 2011, Leslie *et al.* 2014). However, other studies indicated limited spillover from forests into neighbouring arable fields (Ferrante *et al.* 2017, Knapp *et al.* 2019). These inconsistent results suggest that insect pest and weed control potential may be related to habitat productivity, agricultural practices, farming methods, landscape heterogeneity, and species traits and identity (Gayer *et al.* 2019, Jowett *et al.* 2019, Knapp *et al.* 2019, Boetzl *et al.* 2020).

Based on our results, forest edges under continued anthropogenic influence were equally permeable for ground beetle species of all sizes, and they could easily invade the forest interiors. Their invasion may adversely affect the forest interior specialists (Kromp 1999, Magura *et al.* 2010, Magura *et al.* 2020), the composition and organisation of forest interior communities (Paillet *et al.* 2010, Tscharntke *et al.* 2012, Magura *et al.* 2018, Fenoglio *et al.* 2020), and even ecosystem functions and services (Tscharntke *et al.* 2012, Eötvös *et al.* 2018, Eötvös *et al.* 2020, Magura & Lövei 2020*a*). Therefore, human-created and maintained edges should be restored (by softening these edges, Samways 2007) to develop a filter function similar to natural edges, ensuring continued ecosystem functions and services in forest fragments.

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APPENDIX

Table S1. Publications used in the meta-analyses, which reported mean values of abundances, standard deviation, and sample size for both the forest interior and the forest edge.

Edge type	Human disturbance	Country	Reference
natural	none	Hungary	Elek & Tóthmérész 2010
natural	none	Italy	Lacasella *et al.* 2015
natural	none	Hungary	Magura 2002
natural	none	Hungary	Magura & Tóthmérész 1997
natural	none	Hungary	Magura & Tóthmérész 1998
natural	none	Hungary	Magura *et al.* 2000
natural	none	Hungary	Magura *et al.* 2001
natural	none	Hungary	Magura *et al.* 2002
natural	none	Romania	Máthé 2006
natural	none	Hungary	Molnár *et al.* 2001
natural	none	Hungary	Tóthmérész *et al.* 2014
disturbed	agriculture	UK	Bedford & Usher 1994
disturbed	agriculture	New Zealand	Ewers 2008
disturbed	agriculture	Japan	Kagawa & Maeto 2009
disturbed	agriculture	Japan	Kagawa & Maeto 2014
disturbed	agriculture	South Africa	Kotze & Samways 1999
disturbed	agriculture	Poland	Sklodowski 1999
disturbed	agriculture	Spain	Taboada *et al.* 2004
disturbed	agriculture	China	Yu *et al.* 2007
disturbed	forestry	Australia	Davies & Margules 1998
disturbed	forestry	Belgium	Gaublomme *et al.* 2013
disturbed	forestry	USA	Halaj *et al.* 2008
disturbed	forestry	Finland	Heliölä *et al.* 2001
disturbed	forestry	Canada	Lemieux & Lindgren 2004
disturbed	forestry	Canada	Phillips *et al.* 2006
disturbed	forestry	Canada	Spence *et al.* 1996
disturbed	forestry	USA	Ulyshen *et al.* 2006
disturbed	forestry	China	Yu *et al.* 2009
disturbed	urbanisation	Belgium	Gaublomme *et al.* 2008
disturbed	urbanisation	Belgium	Gaublomme *et al.* 2013
disturbed	urbanisation	USA	Silverman *et al.* 2008

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Table S2. Lists of species from the 30 published papers used in the meta-analyses, and their body sizes (L = large, M = medium, S = small), habitat affinity (F = forest, G = generalist, O = open-habitat), wing form (B = brachypterous, D = dimorphic, M = macropterous) and breeding type (AB = autumn breeder, SB = spring breeder, SB & AB = spring and autumn breeder). NA = not available

Species	Body size	Habitat affinity	Wing form	Breeding
Abax carinatus	L	G	B	AB
Abax ovalis	L	F	B	SB
Abax parallelepipedus	L	G	B	SB & AB
Abax parallelus	L	F	B	SB
Abax schueppeli	L	F	B	NA
Acupalpus sp.	S	NA	NA	NA
Acupalpus testaceus	S	O	M	NA
Agonum aeruginosum	S	G	M	SB
Agonum afrum	S	G	M	SB
Agonum decorum	S	G	M	SB
Agonum duftschmidi	S	G	M	SB
Amara aenea	S	O	M	SB
Amara anthobia	S	G	M	SB
Amara convexior	S	G	M	SB
Amara curta	S	O	M	SB
Amara equestris	M	O	M	AB
Amara eurynota	M	O	M	AB
Amara familiaris	S	O	M	SB
Amara macronata	M	G	M	AB
Amara montivaga	S	O	M	SB
Amara nitida	S	O	M	SB
Amara obesa	M	O	D	AB
Amara ovata	S	F	M	SB
Amara saphyrea	M	F	M	SB
Amara sicula	M	O	B	NA
Anisodactylus binotatus	M	O	M	SB
Anisodactylus punctatipennis	M	G	NA	SB
Aptinus bombarda	M	F	B	SB
Aristochroa gratiosa	L	F	NA	NA
Asaphidion flavipes	S	O	M	SB

Table S2 (continued)

Species	Body size	Habitat affinity	Wing form	Breeding
Badister bullatus	S	G	M	SB
Badister lacertosus	S	G	M	SB
Badister meridionalis	S	O	M	SB
Bembidion grapii	S	O	D	SB
Bembidion guttula	S	G	D	SB
Bembidion lampros	S	G	D	SB
Bembidion oblongulum	S	F	B	NA
Bembidion tetracolum	S	G	D	SB
Brachinus alternans	L	G	M	SB
Calathus advena	M	F	M	AB
Calathus cinctus	S	O	D	AB
Calathus fuscipes	M	O	B	AB
Calathus ingratus	M	F	D	SB
Calathus melanocephalus	S	O	D	AB
Calosoma chinense	L	G	M	AB
Calosoma davidis	L	O	NA	NA
Calosoma tepidum	L	O	M	SB
Carabus arvensis	L	G	B	SB
Carabus auronitens	L	F	B	SB
Carabus cancellatus	L	G	B	SB
Carabus convexus	L	G	B	SB
Carabus coriaceus	L	F	B	AB
Carabus glabratus	L	F	M	AB
Carabus granulatus	L	G	D	SB
Carabus hampei	L	G	B	NA
Carabus hortensis	L	F	B	AB
Carabus intricatus	L	F	B	SB
Carabus limbatus	L	F	B	SB
Carabus lineatus	L	F	B	NA
Carabus linnei	L	F	B	NA
Carabus marginalis	L	F	B	NA
Carabus montivagus	L	G	B	AB
Carabus nemoralis	L	G	B	SB

Table S2 (continued)

Species	Body size	Habitat affinity	Wing form	Breeding
Carabus obsoletus	L	F	B	NA
Carabus problematicus	L	F	B	AB
Carabus shamaevi	L	G	NA	NA
Carabus sylvosus	L	G	B	AB
Carabus taedatus	L	O	B	NA
Carabus ullrichii	L	G	B	SB
Carabus variolosus	L	F	B	SB
Carabus violaceus	L	F	B	SB
Carabus yaconinus	L	G	B	SB
Carabus zawadszkii	L	F	B	NA
Chlaenius abstersus	L	G	M	NA
Chlaenius aestivus	L	F	D	SB
Chlaenius erythropus	L	F	M	SB
Chlaenius naeviger	L	G	M	SB
Chlaenius sericimicans	L	G	NA	SB
Cicindela germanica	M	O	M	AB
Cicindela longilabris	L	O	M	SB & AB
Clivina bipustulata	S	O	M	SB
Clivina fossor	S	O	D	SB
Clivina rubicunda	S	NA	M	NA
Cophosomorpha angulicollis	L	NA	NA	NA
Cychrus attenuatus	L	F	B	AB
Cychrus caraboides	L	F	B	AB
Cychrus italicus	L	F	B	AB
Cychrus okamotoi	L	F	B	NA
Cychrus spinicollis	L	F	B	NA
Cychrus tuberculatus	L	F	B	NA
Cyclotrachelus brevoorti	L	F	B	NA
Cymindis axillaris	M	O	D	NA
Cymindis cingulata	S	G	M	NA
Cymindis etrusca	M	O	NA	NA
Dicaelus dilatatus	L	G	B	SB
Dicaelus elongatus	L	G	B	SB

Table S2 (continued)

Species	Body size	Habitat affinity	Wing form	Breeding
Dicheirotrichus cognatus	S	O	M	SB
Diplocheila assimilis	L	F	M	SB
Dyschirius globosus	S	G	B	SB
Elaphrus clairvillei	S	G	M	SB
Galerita bicolor	L	G	M	SB
Galerita sp.	L	G	M	SB
Harpalus affinis	M	O	M	SB & AB
Harpalus attenuatus	S	O	M	NA
Harpalus chalcentus	L	O	M	SB
Harpalus griseus	M	G	M	AB
Harpalus latus	M	G	M	SB & AB
Harpalus pensylvanicus	L	O	M	AB
Harpalus rubripes	M	O	M	SB & AB
Harpalus serripes	M	O	M	SB
Harpalus sinicus	L	G	M	AB
Harpalus sulphuripes	S	O	NA	NA
Harpalus tardus	M	O	M	SB
Harpalus tridens	M	G	M	AB
Hystrichopus praedator	L	NA	NA	NA
Hystrichopus vigilans	L	NA	NA	NA
Laemostenus latialis	L	F	NA	NA
Laemostenus terricola	L	G	B	SB
Lebia chlorocephala	S	O	M	SB
Lebia cyanocephala	S	O	M	SB
Leistus ferrugineus	S	G	M	AB
Leistus fulvibarbis	S	F	M	AB
Leistus piceus	S	G	B	AB
Leistus rufomarginatus	S	F	B	AB
Leistus spinibarbis	M	O	M	AB
Lesticus magnus	L	G	M	SB
Licinus depressus	M	O	B	SB
Licinus italicus	L	F	B	NA
Lophoglossus gravis	L	F	NA	NA

Table S2 (continued)

Species	Body size	Habitat affinity	Wing form	Breeding
Mecodema fulgidum	L	G	NA	NA
Mecodema rugiceps	L	F	NA	NA
Micratopus aenescens	S	NA	NA	NA
Molops piceus	M	F	B	SB
Nebria asturiensis	M	F	B	NA
Nebria brevicollis	M	G	M	AB
Nebria tibialis	M	F	NA	NA
Notiobia terminata	M	O	M	SB
Notiophilus aestuans	S	O	M	SB
Notiophilus biguttatus	S	F	D	SB
Notiophilus palustris	S	G	D	SB
Notiophilus rufipes	S	G	D	SB
Notiophilus sylvaticus	S	O	D	SB
Notonomus variicollis	L	NA	NA	NA
Omus dejeanii	L	F	B	SB
Oodes amaroides	M	G	M	SB
Oxypselaphus obscurus	S	G	D	SB
Panagaeus bipustulatus	S	O	M	SB
Paratachys sp.	S	NA	M	SB
Paraxinidium andreaei	S	NA	NA	NA
Piesmus submarginatus	M	F	NA	NA
Platyderus neapolitanus	S	F	NA	NA
Platyderus rufus	S	G	B	AB
Platynus assimilis	M	F	M	SB
Platynus decentis	M	F	M	SB
Platynus krynickii	M	F	M	SB
Platynus magnus	L	G	M	AB
Poecilus chalcites	M	O	M	SB
Poecilus cupreus	M	O	M	SB
Poecilus koyi	M	O	NA	NA
Poecilus lepidus	L	O	D	AB
Poecilus versicolor	M	O	M	SB
Promecognathus crassus	M	G	NA	NA

Table S2 (continued)

Species	Body size	Habitat affinity	Wing form	Breeding
Pseudoophonus rufipes	L	O	M	AB
Pterostichus adstrictus	M	G	M	SB
Pterostichus amethystinus	L	F	NA	NA
Pterostichus anthracinus	M	G	D	SB
Pterostichus brevicornis	S	F	B	AB
Pterostichus burmeisteri	L	F	B	SB
Pterostichus cantaber	L	F	B	NA
Pterostichus cantabricus	S	F	B	NA
Pterostichus castaneus	M	NA	B	NA
Pterostichus cristatus	L	F	B	SB
Pterostichus ebenus	L	G	B	AB
Pterostichus haesitatus	M	F	NA	NA
Pterostichus haptoderoides	S	G	M	SB
Pterostichus herculaneus	L	F	B	AB
Pterostichus hungaricus	L	G	B	NA
Pterostichus inanis	M	F	NA	NA
Pterostichus lama	L	F	B	NA
Pterostichus lattini	L	F	B	SB
Pterostichus madidus	L	F	B	AB
Pterostichus melanarius	L	G	D	AB
Pterostichus melas	L	G	B	NA
Pterostichus micans	L	F	NA	NA
Pterostichus microcephalus	M	G	M	AB
Pterostichus niger	L	G	M	AB
Pterostichus oblongopunctatus	M	F	M	SB
Pterostichus ovoideus	S	G	D	SB
Pterostichus pohnerti	M	NA	NA	NA
Pterostichus protractus	L	F	NA	SB
Pterostichus riparius	S	F	B	NA
Pterostichus strenuus	S	G	D	SB
Pterostichus sulcitarsis	S	G	M	SB
Pterostichus trinarius	L	F	B	SB
Pterostichus tuberculofemoratus	M	F	NA	NA

Table S2 (continued)

Species	Body size	Habitat affinity	Wing form	Breeding
Scaphinotus angulatus	L	F	B	NA
Scaphinotus angusticollis	L	F	B	NA
Scaphinotus marginatus	L	F	B	AB
Scaphinotus rugiceps	L	F	B	NA
Scarites sp.	L	O	M	NA
Semiardistomis viridis	S	NA	M	NA
Sericoda bembidioides	S	G	M	NA
Sericoda quadripunctata	S	F	M	SB
Stenolophus ochropezus	S	G	M	SB
Stomis pumicatus	S	G	B	SB
Syntomus americanus	S	O	D	SB
Syntomus foveatus	S	O	B	SB
Syntomus pallipes	S	G	B	SB
Syntomus truncatellus	S	G	B	SB
Synuchus arcuaticollis	M	G	B	AB
Synuchus cycloderus	M	F	M	AB
Synuchus dulcigradus	M	F	M	AB
Synuchus impunctatus	M	G	D	AB
Synuchus nitidus	L	F	D	AB
Synuchus vivalis	S	O	D	AB
Trachypachus holmbergi	S	O	NA	SB
Trechus chalybeus	S	G	B	SB & AB
Trechus obtusus	S	O	D	SB
Trechus quadristriatus	S	O	D	AB
Trichotichnus nitens	S	F	NA	NA
Zacotus matthewsii	L	F	B	NA

Table S3. Estimates and heterogeneities in the models.

Abundance of small species								
Subgroup	Mean effect size (model)	Lower CI bound (model)	Upper CI bound (model)	SE (model)	p value (model)	Q (hetero-geneity)	p value (hete-ro-ge-neity)	I^2
Edges with human influences	-0.340	-0.609	-0.072	0.137	0.013	93.364	<0.001	54%
Edges with natural processes	-0.280	-0.471	-0.089	0.097	0.004	83.969	0.249	9%
Overall	-0.293	-0.375	-0.211	0.042	<0.001	177.780	<0.001	33%
Edges disturbed by agriculture	-0.482	-1.195	0.230	0.363	0.184	1.889	0.864	0%
Edges disturbed by forestry	-0.312	-0.829	0.204	0.263	0.236	84.208	<0.001	60%
Overall	-0.243	-0.460	-0.026	0.111	0.028	87.061	<0.001	54%
Component of variance	Q	$d.f.$	p		Component of variance	Q	$d.f.$	p
Edges with human influences	93.364	43	<0.001		Edges disturbed by agriculture	1.889	5	0.864
Edges with natural processes	83.969	76	0.249		Edges disturbed by forestry	84.208	34	<0.001
Within	177.333	119	<0.001		Within	86.097	39	<0.001
Between	0.130	1	0.718		Between	0.143	1	0.705
Total	177.780	120	<0.001		Total	87.061	40	<0.001

Table S3 (continued)

Abundance of medium species								
Subgroup	Mean effect size (model)	Lower CI bound (model)	Upper CI bound (model)	SE (model)	*p* value (model)	*Q* (hetero-geneity)	*p* value (het-eroge-neity)	I^2
Edges with human influences	-0.179	-0.514	0.155	0.171	0.294	82.473	<0.001	58%
Edges with natural processes	0.115	-0.154	0.385	0.138	0.402	211.700	<0.001	71%
Overall	-0.057	-0.191	0.077	0.068	0.405	304.732	<0.001	68%
Edges disturbed by agriculture	0.312	-0.780	1.404	0.557	0.576	9.979	0.352	10%
Edges disturbed by forestry	-0.247	-0.892	0.397	0.329	0.452	72.395	<0.001	68%
Overall	-0.235	-0.540	0.069	0.155	0.130	82.433	<0.001	60%
Component of variance	*Q*	*d.f.*	*p*		Component of variance	*Q*	*d.f.*	*p*
Edges with human influences	82.473	35	<0.001		Edges disturbed by agriculture	9.979	9	0.352
Edges with natural processes	211.700	61	<0.001		Edges disturbed by forestry	72.395	23	<0.001
Within	294.173	96	<0.001		Within	82.374	32	<0.001
Between	1.806	1	0.179		Between	0.748	1	0.3873
Total	304.732	97	<0.001		Total	82.433	33	<0.001

Table S3 (continued)

Abundance of large species

Subgroup	Mean effect size (model)	Lower CI bound (model)	Upper CI bound (model)	SE (model)	*p* value (model)	*Q* (hetero-geneity)	*p* value (het-eroge-neity)	I^2
Edges with human influences	0.132	-0.138	0.402	0.138	0.339	207.061	<0.001	59%
Edges with natural processes	-0.230	-0.503	0.044	0.140	0.100	845.862	<0.001	81%
Overall	-0.184	-0.278	-0.091	0.048	<0.001	1085.067	<0.001	77%
Edges disturbed by agriculture	-0.118	-0.710	0.474	0.302	0.696	86.713	<0.001	67%
Edges disturbed by forestry	0.310	-0.309	0.928	0.316	0.326	66.844	0.015	34%
Edges disturbed by urbanisation	0.712	-0.434	1.858	0.585	0.223	23.368	0.001	74%
Overall	0.022	-0.152	0.195	0.088	0.808	192.976	<0.001	58%
Component of variance	*Q*	*d.f.*	*p*		Component of variance	*Q*	*d.f.*	*p*
Edges with human influences	207.061	85	<0.001		Edges disturbed by agriculture	86.713	29	<0.001
Edges with natural processes	845.862	160	<0.001		Edges disturbed by forestry	66.844	44	0.015
Within	1052.923	245	<0.001		Edges disturbed by urbanisation	23.368	6	0.001
Between	3.399	1	0.0652		Within	176.925	79	<0.001
Total	1085.067	246	<0.001		Between	1.848	2	0.397
					Total	192.976	81	<0.001

Table S4. Results of regression tests for funnel plot asymmetry of abundances of small, medium and large ground beetle species.

	Weighted regression		Mixed-effects meta-regression	
Small species	$t_{1,119} = -2.6516$	$p = 0.0091$	$z = -3.1028$	$p = 0.0019$
Medium species	$t_{1,96} = -1.2362$	$p = 0.2194$	$z = -0.7209$,	$p = 0.4710$
Large species	$t_{1,245} = 2.2258$	$p = 0.0269$	$z = 2.4235$	$p = 0.0154$

Table S5. Model results after trim and fill for the abundances of small, medium and large ground beetle species.

	Estimated missing studies	Estimate (Hedges' *g*)	Lower CI bound	Upper CI bound	SE	*p* value
Small species	24 (SE = 7.2210)	-0.1938	-0.2745	-0.1130	0.0412	<0.0001
Medium species	13 (SE = 6.4483)	0.0841	-0.0628	0.2311	0.0750	0.2618
Large species	0 (SE = 8.6527)	-0.1820	-0.2805	-0.0835	0.0503	0.0003

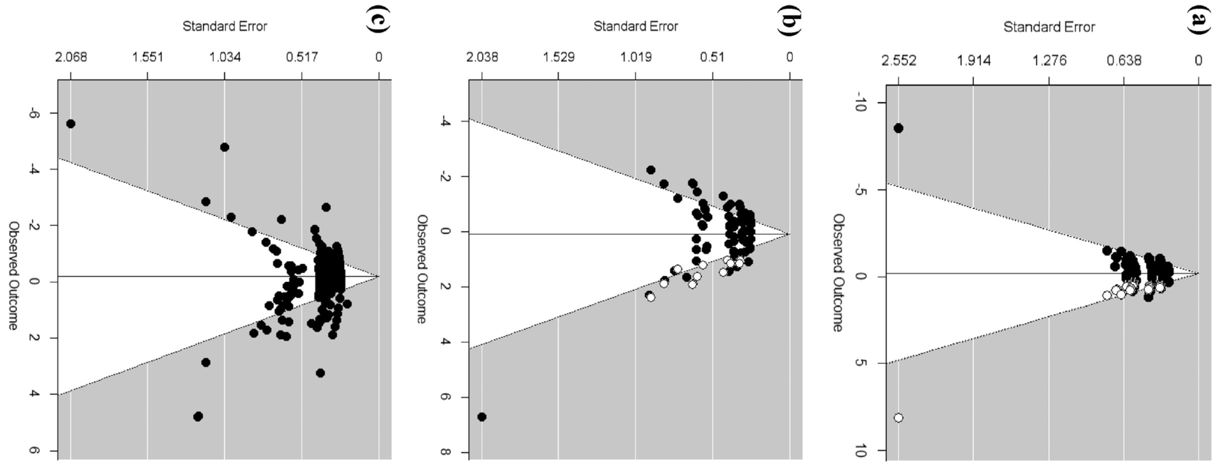

Fig. S1. Funnel plots of the abundance of small (a), medium (b), and large ground beetle species (c) with missing studies (empty circles) estimated by the trim and fill method