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RESEARCH ARTICLE

Matrix type affects carabid beetle community and trait composition, and intraspecific variation in remnant forests

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Abstract

Aim: The Anthropocene is characterised by urban and agricultural landscapes. Within these landscapes, natural to semi-natural habitats are fragmented, isolated and disturbed to varying degrees. Species associated with these natural habitats have to content with the surrounding landscape, both in terms of level of isolation, and matrix type and quality. We investigated the community structure, trait distribution and individual traits of carabid beetles in boreal forest fragments within three matrices: urban, agricultural and freshwater lake.

Location: City of Lahti and its surroundings, southern Finland.

Taxon: Coleoptera, Carabidae.

Methods: Using pitfall traps from June to October 2019, we collected carabid beetles from eight spruce-dominated forest fragments in the urban matrix, 10 fragments in an agricultural matrix, seven fragments on lake islands and three large control forests at the outskirts of the city.

Results: Compared to natural forests, carabid beetles in forest fragments in these matrices showed distinct assemblages, and with beetle diversity the highest in fragments in the agricultural landscape. Fragments in the urban and lake island landscapes were characterised by small-sized species, and those capable of flight. We also found strong intraspecific trait responses in terms of body size, with some generalist species being significantly smaller in urban, agricultural or lake island fragments compared to the controls.

Main Conclusions: The matrix has a clear effect on carabid beetle communities, both in terms of taxonomic and trait distribution, and filters for communities of smaller sized species and those capable of flight. Such overall community and intraspecific effects can have considerable effects on populations and community assemblages: As anthropogenic effects intensify in urban and agricultural landscapes, our findings may be the expression of further morphological and physiological responses, and eventually in the adaptation of those species that can cope with the Anthropocene.

KEYWORDS
agriculture, ground beetle, lake, urban

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1 | INTRODUCTION

Nature is fragmented in a plethora of ways. In terrestrial systems, this is clearly visible in urban and agricultural landscapes where natural to semi-natural habitats are surrounded by constructed grey spaces or agriculture. Recently, Uhler et al. (2021) argued that urbanisation and agriculture are major drivers of insect decline. Natural fragments in these anthropogenic landscapes, such as remnant forests, are exposed to development in their surroundings (the matrix), increasing fragmentation and isolation and decreasing fragment size and quality. The literature is replete with examples on the effects of fragment size, isolation and habitat quality on taxa within these habitats (e.g. Beninde et al., 2015; Fahrig, 2003; Harris, 1984; Rodewald, 2003), and our theoretical understanding of the processes involved in species occupancy and diversity in these fragments is well established (island biogeography theory, metapopulation dynamics, landscape processes, etc.). What is less well understood is the influence of the surrounding matrix on taxa within these fragments (but see Fahrig, 2001; Martin & Fahrig, 2015), especially in comparing different types of matrices on organisms, at both the community and intraspecific levels. Here, we investigate the effects of three types of landscape matrices, urban, agriculture and freshwater lake, on carabid beetle communities in spruce-dominated forest fragments within such landscapes.

Remnant forests in anthropogenic environments are often characterised by a sharp transition between habitat and non-habitat. These sharp edges, together with the relatively small sizes of remnant habitat in cities and agricultural landscapes, expose insular communities to altered biotic and abiotic conditions in the matrix (Rand & Louda, 2006; Sisk et al., 1997). Fahrig (2001), in a spatially explicit simulation model exercise, showed that less than half of the focal habitat is required for population persistence if the quality of the matrix is converted from 'very low' to 'very high'. Clearly, apart from intrinsic features of a habitat, such as patch size, isolation and quality, characteristics of the landscape can have a strong effect on taxa within habitats. Since one of the largest drivers of biodiversity loss is land-use change, particularly due to agricultural and urban expansion (IPBES, 2019), a better understanding of the effects of the matrix on taxa within greenspaces is needed to advance our theoretical understanding of insular communities, and to provide management recommendations for the preservation of biodiversity in these landscapes.

Our understanding of the response of nature to human-dominated landscapes has advanced substantially with the development of a trait-based approach (Moretti et al., 2017). Traits can be categorised into, for example, morphological, feeding, life history, physiological and behavioural, and can be linked to the function an organism performs (for instance, the proboscis lengths of lepidopterans are associated with the features of flowering plants they pollinate), or to its occupancy in a particular landscape (for instance, urban environments are characterised by larger bodied mammal, orthopteran and macro-moth species in the community, but smaller sized ground spiders, ground beetles and weevils [Hantak et al., 2021; Merckx et al., 2018]). Incorporating a trait-based approach to the effects of the landscape on taxa occupying greenspace fragments within these landscapes will help us in identifying those types of species vulnerable to fragmentation, and the role of the matrix in filtering species based on the characteristics of the species. Most studies that have used a trait-based approach have done so at the community level where species are assigned mean trait values of interest (Hahs et al., 2023). However, intraspecific trait variability is of particular importance since phenotypically diverse individuals of a species can indicate environmental/disturbance gradients in the landscape that are not picked up by using mean trait values (see Bolnick et al., 2011; Moretti et al., 2017). For instance, Sadler et al. (2006) showed that the carabid beetles *Pterostichus madidus* and *Abax parallelepipedus* increased in body length along a rural to urban woodland gradient in Birmingham, United Kingdom, while Weller and Ganzhorn (2004) showed that *Carabus nemoralis* decreased in body length towards the city centre (Hamburg, Germany). Such changes in intraspecific trait variation, brought about, for instance, by human actions (see Des Roches et al., 2018; Palkovacs et al., 2012), can also be expected to result in significant effects on ecological processes.

Our main aim was to investigate the effects of starkly different landscapes on the carabid beetle communities in indigenous forest of similar type embedded within these matrices, which have different isolating effects on the beetle communities. We selected forest fragments of varying size within an urban landscape, an agricultural landscape and a freshwater lake-island landscape. Additionally, we selected three large forest fragments at the outskirts of the city of Lahti, southern Finland, which acted as reference habitat. We expect these landscapes to filter the carabid beetle community differently due to their matrix character; for instance, a lake matrix offers no opportunity for species to disperse between forested lake islands except via flight, or the occasional introduction due, for example, to drift (see Bell et al., 2017; Kotze & Niemelä, 2002). The urban matrix is also expected to be severe (see Nielsen et al., 2014), with substantial losses in individuals due to foot and road traffic and a highly hostile (also in terms of microclimate) ground surface (roads, buildings, pavements, etc.). The agricultural matrix may appear less hostile to these beetles; however, generalist and open-habitat species may penetrate into the edges of these fragments, competing with forest species, thus affecting their abundances or presence negatively. Given these processes, we hypothesise that (1) communities in forest fragments situated on lake islands, in the city and in an agricultural landscape will show distinct community structures, since these communities are likely affected differently by beetle communities and the abiotic environment in the surrounding matrix, and will be separate from those in large reference forests that are likely to be affected less by the surrounding landscape. (2) If positive species–area relationships are observed in these landscapes, the agricultural landscape will display greater richness across fragment size due to the potential for generalist species to disperse into the forest fragments from the agricultural matrix (Koivula et al., 2004). However, fragments in these landscapes are typically small, which may result in no relationship between fragment size and species richness (the so-called small-island effect; Lomolino & Weiser, 2001). (3) Compared to the large control forests, carabid beetle communities in fragments in the city, on lake islands and in the agricultural landscape are expected to consist of a higher number of flight capable species, smaller sized species and overall generalists. (4) Finally, if fragments in the city in particular, but also on lake islands and in the agricultural matrix, experience acute disturbances that affect beetle development (see Chown & Gaston, 2010; Tseng et al., 2018), we hypothesise intraspecific effects so that individual species will differ in their size in these fragments, and are predicted to be smaller, compared to individuals inhabiting control forests.

2 | MATERIALS AND METHODS

The study was performed within the city of Lahti, southern Finland (60°58'57.45 "N, 25°39'40.42" E) and its outskirts. Indigenous, spruce-dominated (*Picea abies*) forest fragments of varying size were selected in three matrices: urban ($n=8$, 0.08–21.1 ha), agricultural ($n=10$, 0.06–14.2 ha) and lake ($n=7$, 0.10–48.2 ha). All fragments selected were at least 70 years of age or older. Additionally, we selected three large (ca. 400–600 ha) protected control forests, each ca. 100 y of age, at the outskirts of the city (https://www.google.com/maps/d/viewer?mid=1yfXKDPNiAPZTb5pAeLI8pkcMRMhXU-QN&ll=60.97618402244856%2C25.622075702995062&z=10, see also Appendix S1, Table S1). Distances between fragments within a matrix type are as follows: control forests (mean = 4.9 km, maximum = 8.3 km, minimum = 1.1 km), agricultural (14.2 km, 28.6 km, 0.3 km), urban (1.7 km, 4.4 km, 0.2 km), lake (1.8 km, 4.5 km, 0.2 km).

Carabid beetles were collected from 6 June to 18 October 2019, using plastic pitfall traps (mouth diameter = 65 mm). Trapping was continuous, visiting and retrieving the catch every third to fourth week (four to six visits). A single year of sampling the carabid beetle community can be a limitation due to annual variation, yet communities are unlikely to change drastically in the short term, but more so in the long term (Kotze & Niemelä, 2002). The traps were half filled with a 50% aqueous propylene glycol-water solution to preserve the catch and covered with brown 10 cm × 10 cm plastic roofs to protect the catch from excess debris and rain. Traps were placed ca. 10 m apart in a zigzag manner within each fragment. The number of traps per fragment depended on the size of the fragment, but with a minimum of five traps placed in the smallest fragments and a maximum of 10 traps in the largest fragments and control forests. Trap losses per visit (see Appendix S1, Table S1) were accounted for into the statistical analyses. The carabid beetles collected were identified using keys in Lindroth (1985, 1986), with updated names confirmed by specialists at the Finnish Museum of Natural History (https://www.luomus.fi/en). Carabid beetle trait information were measured or collected from the literature. We measured the total length (tip of the head to the tip of the elytra, in mm), elytra length (mm) and wing morphology (constantly short-winged species [apterous or brachypterous], constantly long-winged species [macropterous], species with both short- and long-winged individuals [dimorphic]) of all individuals collected. Total beetle length correlated highly with elytra length ($r=0.987$, $y=0.609x - 0.345$, $n=2401$; 13 specimens were damaged and could not be measured) and we used elytra length in all subsequent analyses as we assumed less error in measuring this feature. Trait information obtained from various literature sources included specialisation level (strict specialist, average specialist, average specialisation, average generalist, true generalist), moisture preference (wet, dry), habitat association (woodland, open, many, riparian), environmental tolerance (associated with human environments or not) and feeding (predator, granivore, omnivore) (Kotze & O'Hara, 2003; Lindroth, 1985, 1986; Nolte et al., 2019). Although not straightforward, specialisation level in the study of carabid beetles can be used as a general concept that includes niche breadth, habitat affinity and various microhabitat preferences (see Kotze et al., 2003; Kotze & O'Hara, 2003). We also counted the number of spider, ant and snail individuals collected.

To characterise the local environment, the following variables were recorded from each of the 28 forest fragments (see Appendix S1, Table S2). Five measurements of canopy cover (as a percentage) were recorded along the transects and averaged in the analyses. Five 1 m × 1 m squares were placed along each transect per fragment, with percentage field layer, percentage ground layer and litter layer depth (3 measurements per quadrat, in cm) recorded. Soil samples were collected from outside the quadrats and mixed into a plastic bag to make a composite sample for each fragment. The top 5 cm of soil was collected using a plastic scoop. After sieving the soils through a 2-mm sieve, we calculated percentage soil moisture, percentage organic matter (OM) and pH from these samples. Fifteen grams of wet soil was placed in an oven (70°C) for 24 h to determine soil moisture. A portion of these dried soils was incinerated in a muffle oven at 550°C for 5 h to analyse percentage OM.

Statistical analyses were performed in R version 4.2.2 (R Core Team, 2022). To compare species richness between the four landscapes, we performed rarefaction using the rarefy function in the 'vegan' package, version 2.6–4. We investigated the effect of fragment size on carabid beetle species richness by constructing species–area relationship curves. Three species richness measures were used: uncorrected number of species per fragment, and the Chao1 and ACE indices. Both indices are nonparametric methods for estimating the number of species in the community but with Chao1 placing more weight on rare species in estimating richness, while ACE estimating the number of species using sample coverage, that is, the sum of the probabilities of the observed species (see Gotelli & Colwell, 2011). To visualise carabid beetle community structure in the 28 fragments, a non-metric multidimensional scaling (NMDS) ordination was performed on the standardised catch per fragment. The catch per species per fragment was standardised by dividing the total catch of that species in the fragment by the number of trapping days (number of traps x active trap days) of that forest fragment, multiplied by 1000. The metaMDS function in the 'vegan' package (Oksanen et al., 2020) was used to perform this analysis, using the Bray–Curtis dissimilarity metric. Using the mrpp function, a multiresponse permutation procedure (MRPP) was performed to test for differences in carabid beetle community structure between the four landscapes sampled. MRPP returns a T statistic (which describes the separation between groups, here landscapes: the more negative T, the stronger the separation) (McCune et al., 2002).

To evaluate the response of carabid beetle traits to the environment in these landscapes, we performed a fourth-corner and RLQ analysis, which links traits to the environment, via beetle abundances (Brown et al., 2014; Dray et al., 2014), using the 'ade4' package, version 1.7.22 (Dray & Dufour, 2007). The beetle traits and environmental variables used in this analysis are described above. The beetle abundance table used the same standardisation procedure as the NMDS above. The carabid beetle traits used in this analysis represent mean trait values from the literature, or from measurements (wing morphology and elytra length) made on the beetles collected. Generalised linear mixed models (negative binomial error distribution, glmer.nb function in the 'lme4' package, version 1.1.34) were used to test for differences in the counts of species with different elytra lengths and wing types within each of the landscape types investigated. Body size was categorised as small (1–5 mm, elytra length), medium (>5–10 mm) and large (> 10 mm), while wing type was categorised as brachypterous, dimorphic and macropterous. Site (forest fragment) was added as a random term to account for differences in the number of species collected per fragment. Lastly, GLMs were used to test for intraspecific variation in elytra length across the four landscape types of those species for which a sufficient number of individuals were collected. Initially, we constructed a single linear mixed effects model in which landscape type and fragment size were included as predictor variables, and the eight most abundantly collected species were included as a random term. The model returned significant landscape type effects, but the variance explained by the predictor variables was poor (see Appendix S1, Table S3). Subsequently, we evaluated each species separately, including landscape type and fragment size as predictor variables. The Levene's test was used to calculate the equality of variances in elytra length of individual species between the landscape types. Elytra length data were log-transformed to satisfy assumptions of normality where necessary.

3 | RESULTS

A total of 47 species, including 2414 individuals, were collected. *Pterostichus melanarius* was the most abundant species with 42.5% of the catch, followed by *Carabus nemoralis* (14.1%), *P. oblongopunctatus* (7.6%), *Patrobus assimilis/atrorufus* (5.5%) and *Calathus micropterus* (4.5%) (Appendix S1, Table S1). Agricultural fragments were the richest in carabid species and control forests the poorest, with urban and lake forest fragments being intermediate (Appendix S2, Figure S1). Species–area relationships (ln–ln) vary across landscapes, but when focusing on forest-associated species only (by excluding open-habitat and generalist species), fragments in the agricultural and urban landscapes show positive relationships, while the relationship on lake islands varies depending on the index used (Figure 1).

3.1 | Community structure and traits

The type of matrix had a clear effect on the carabid beetle communities sampled (Figure 2). Communities within the three control forests were similar to one another, and so too, but to a lesser degree, were communities within forest fragments in the city similar to one another. Communities within fragments in the agricultural and lake island landscapes were more heterogeneous, especially so in the lake landscape, as displayed by the larger ellipses for these landscapes. In terms of community structure, lake island communities were significantly different from all other landscapes (Appendix S1, Table S4). Linking carabid beetle trait distribution to the environment, via beetle abundance (fourth-corner and RLQ analysis) showed the following: The percentage of variance explained by the first RLQ axis was 50.4%, and that by the second axis, 26.4% (Appendix S1, Table S5). In terms of environmental variables measured, fragment type (especially lake island fragments), fragment size, soil moisture, OM and pH contributed substantially (in terms of total inertia) to variance in the data (Figure 3a, Appendix S1, Table S6), while body size, average specialisation and average generalist, an association with wet habitats, a preference for natural environments and a generalist feeding habit contributed substantially to variance in the trait data (Figure 3b, Appendix S1, TableS7). The fourth-corner results (Figure 3d, Appendix S1, Table S6 and S7) revealed some expected results in terms of the association between beetle traits with the measured environment. For instance, fragments in the agricultural landscape were characterised by beetles that are associated with many habitat types and generalist feeders. The larger the fragment in general, the more likely there were beetles associated with wet and natural environmental conditions and less likely with dry and human-dominated (synanthropic) conditions. An increase in ground layer cover was preferred by woodland-associated carabids, but not by habitat generalists. Unsurprisingly, a higher pH affected species tolerant of human environments positively (city soils are often characterised by higher pH values, Pouyat et al., 2020). Finally, an increase in soil moisture and OM was associated with smaller beetle species and affected average generalists negatively.

Although not statistically significant, the following trends were observed in the four landscapes (Figure 3a,b). The large control forests were characterised by soils with higher % moisture and OM. Beetle traits associated with these forests included those tolerant to natural and wet habitats, and to some degree habitat specialists. Fragments in the agricultural landscape were associated with higher soil pH and more spiders, and beetles that are generalists, wing-dimorphic and to some degree associated with open habitats. Urban fragments were also characterised by a higher pH and more snails, and beetles associated with open and

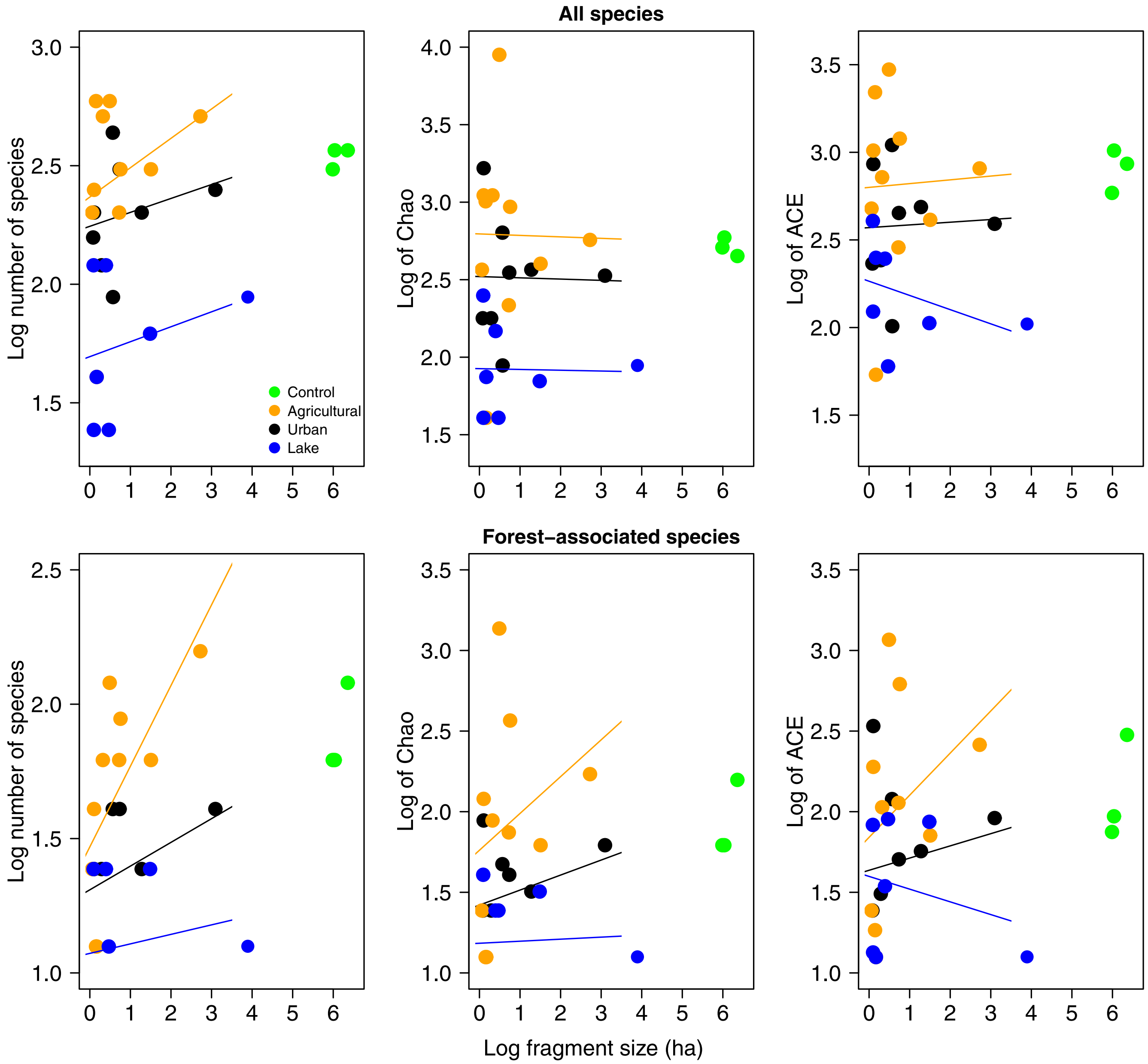


FIGURE 1 Species–area relationships (ln-ln + 1) of carabid beetles in forest fragments in the agricultural, urban and lake landscapes. The log richness of carabid beetles in the three control forests is also shown. Top panels include all species while bottom panels excluded those classified as open-habitat associated and generalist species (see Appendix S1, Table S1). Panels to the left show uncorrected number of species, while the middle panels show Chao1 richness and right panels ACE richness. For regression line statistics, see Appendix S1, Table S1.

dry habitats, and synanthropic species. Lake fragments appeared to have more ants, and beetles with long wings and granivorous feeding.

Focusing on the directly measured traits revealed the following at the community level (Figure 4, Table 1): There were more small-sized than medium- or large-sized species in control forests, but not statistically significantly so. Agricultural forest fragments showed no difference in the count of small-, medium- or large-sized beetles. However, in both urban and lake island fragments, there were significantly fewer large-sized than small- or medium-sized beetles. Forest fragments in the control and agricultural landscapes were characterised by flightless species, more so than dimorphic or macropterous species (except that agricultural forests also consisted of a higher count of macropterous species). Both urban and lake forests had fewer flightless species than dimorphic and macropterous species, significantly so for macropterous species in urban fragments.

3.2 | Intraspecific differences in body size

Fragment size did not explain variation in elytra size and was removed from all models. Some abundantly collected species showed significant intraspecific variation in size across the landscapes (Figure 5, Table 2). For instance, *Carabus nemoralis* was significantly smaller in

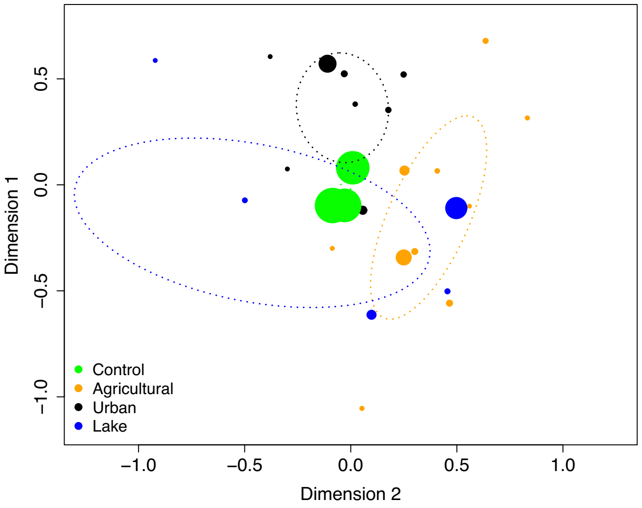


FIGURE 2 Non-metric multidimensional scaling plot displaying the carabid beetle community structure in each fragment (and in the three control forests) in two-dimensional space. The size of the circles reflects the size of the fragment (log (size in ha) + 2). The ellipses are based on standard deviations of the points with 95% confidence intervals.

agricultural and urban fragments compared to control forests, while *Pterostichus melanarius* was significantly smaller in urban and lake island forests compared to control forests and agricultural fragments. These statistically significant differences in mean size are clearly displayed by the number of individuals that were smaller in agricultural, urban and lake forests (the grey dots in Figure 5). *Pterostichus oblongopunctatus* increased in size from control forests to urban and lake fragments. None of the individual species analysed, apart from *P. oblongopunctatus*, showed statistical departure in equality of variance (Levene's test, Table 2).

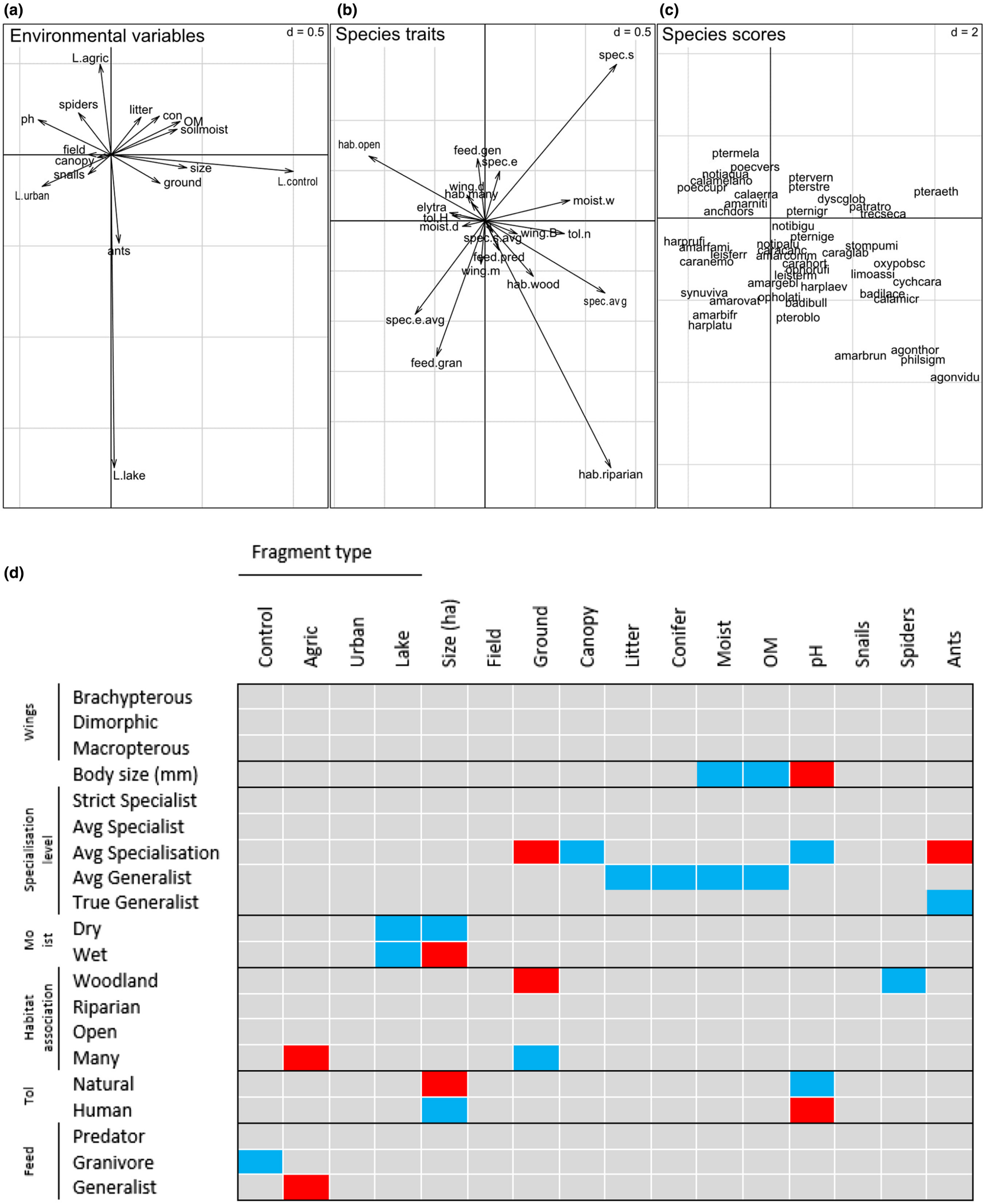
4 | DISCUSSION

The fragmentation of boreal forests in different anthropogenic and natural landscapes affected carabid beetle diversity, community structure and trait distribution. We showed that forest fragments in an agricultural landscape hosted more species than fragments in urban and lake islands, the last of which were species poor. Large control forests were species poor, a general feature for carabid beetles in boreal forests (Niemelä et al., 2007 and references therein). This is due to a lack of true forest specialists in boreal forests (Niemelä, 1997), likely a consequence of the notion that only a few species adapt to consistently adverse environments (Greenslade, 1983), and the fact that species-rich genera (e.g. *Amara*, *Harpalus*) are generally open-habitat to generalist species (Lindroth, 1985, 1986). In essence, forest fragments as terrestrial habitat islands in the boreal landscape are more diverse in carabid beetles, and this is primarily because of the matrix that host generalist species that use these fragments. Furthermore, forest fragments can host larger populations of forest specialists that can use the matrix for supplemental resources (see below), decreasing extinction risks in these fragments.

We also showed that the matrix clearly structured the beetle community, both taxonomically (the NMDS results) and in terms of traits (RLQ and fourth-corner results), confirming earlier studies on the importance of the matrix (Fahrig, 2001; Noreika & Kotze, 2012; Prevedello & Vieira, 2010; Ricketts, 2001; Rodewald, 2003). Beetle size and dispersal ability (wing form) respond at the community level; few large-sized species were collected from forest fragments in the city and on lake islands, but these landscapes were also characterised by highly dispersive species. Finally, we showed clear intraspecific effects on beetle body size, with several species having significantly smaller sized individuals in urban, agricultural and/or lake landscapes compared to the controls, but also the opposite, with a few species being larger in some of these landscapes compared to the control. Overall, our findings provide strong evidence of the effects of the surrounding landscape matrix on insular beetle communities, both at the community and intraspecific levels. Since urbanisation and agriculture are major drivers of insect decline (Uhler et al., 2021), our understanding of the effects of these landscapes on natural to semi-natural habitat within them warrants consideration in biodiversity and conservation research. These large-scale land use expansions are expected to create ever more insular communities that will have significant effects on the occupancy and survival of species in the remaining fragmented and isolated landscape. This will result in the increasing importance of landscape matrices and their qualities (Fahrig, 2001) on the fate of biodiversity in much of human-dominated nature.

4.1 | Effects of the matrix on community structure and traits

The higher species richness in fragments in the agricultural landscape does not appear to be the result of open-habitat species invading these forests from the agricultural matrix, since these forests were also richer in forest-associated species. A potential explanation for this is the quality of the matrix in terms of resource provision. Numerous studies have shown that both predacious and granivorous carabid beetles contribute to biocontrol in agricultural landscapes (Cividanes, 2021; De Heij & Willenborg, 2020; Kromp, 1999), thus potentially providing supplemental resources to forest-associated beetles in adjacent habitat (Knapp et al., 2019; Koivula et al., 2004). This spill-over, or ecological flow of individuals across edges into adjacent environments, thus provides access to supplementary resources (see Ries et al., 2004), primarily for carabid beetles in forest patches in the agricultural landscape. Consequently, forest or generalist species in these forest fragments are less likely to go locally extinct if individuals can move to and from these highly contrasting (see Noreika & Kotze, 2012; Prass et al., 2017; Ries et al., 2004), but resource-rich agricultural matrices. In comparison, the urban and especially the lake matrix likely provide little resources for carabid beetles, further supporting the notion that matrix quality and



		Control	Agric	Urban	Lake	Size (ha)	Field	Ground	Canopy	Litter	Conifer	Moist	OM	pH	Snails	Spiders	Ants
Wings	Brachypterous																
	Dimorphic																
	Macropterous																
	Body size (mm)											🟦	🟦	🟥			
Specialisation level	Strict Specialist																
	Avg Specialist																
	Avg Specialisation							🟥	🟦					🟦			🟥
	Avg Generalist									🟦	🟦	🟦	🟦				
	True Generalist																🟦
Mo ist	Dry				🟦	🟦											
	Wet				🟦	🟥											
Habitat association	Woodland							🟥								🟦	
	Riparian																
	Open																
	Many		🟥					🟦									
Tol	Natural					🟥								🟦			
	Human					🟦								🟥			
Feed	Predator																
	Granivore	🟦															
	Generalist		🟥														

FIGURE 3 RLQ and fourth-corner results. The top panels display the first two axes of the RLQ analysis of the coefficients for environmental variables (a), species traits (b) and the scores of species (c). For more details on the environmental variables and traits used, see Appendix S1, Tables S6 & S7. The *d* values in the plots give the grid size. The bottom panel (d) presents the results of the fourth-corner tests, showing all possible bivariate associations between the environmental variables measured (columns) and the beetle traits (rows). Significant ($p < 0.1$) positive associations are presented in red, while significant negative associations are shown in blue.

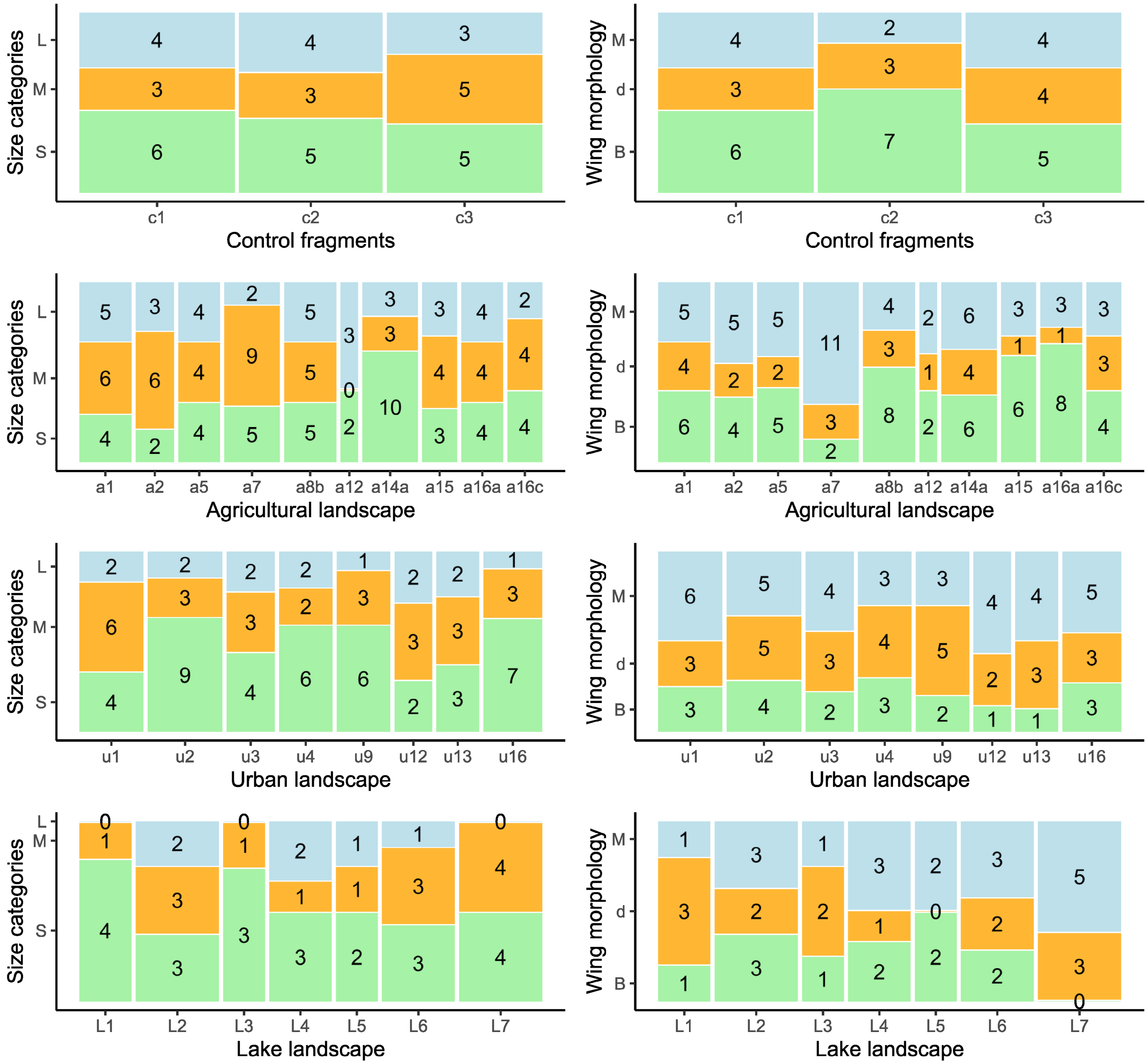


FIGURE 4 The number of small (S), medium-sized (M) and large (L) species (left) and brachypterous (B, short winged or wingless), dimorphic (d, species with both long- and short-winged individuals in the population) and macropterous (M, long-winged) species (right) across the four landscapes investigated. See Table 1 for GLMM test results. The width of each column (fragment) represents the number of species collected in that fragment with numbers representing the number of species per category. The different colours per column represent the proportion of species in that category.

contrast to the focal habitat in question are important to organisms inhabiting patchy environments (Noreika & Kotze, 2012; Prevedello & Vieira, 2010).

The number of species increased with fragment size, but this trend was weaker when correlating Chao1 and ACE diversity indices with fragment size. When focusing on forest-associated carabids, diversity also increased with fragment size, but only in agricultural and urban landscapes. Lövei et al. (2006), studying native forest fragments in Hungary and Ukraine, showed that generalist and edge-preferring carabid species distort the species–area relationship, while focusing on forest specialist species confirms the positive relationship between area and number of species, supporting our findings. However, contrasting relationships for lake islands are difficult to explain, but may be due to a combination of the small-island effect (Lomolino & Weiser, 2001) and the truly insular nature of lake islands compared to fragments embedded in urban and agricultural landscape where the matrix can contribute to the resource use of beetles in these forests and aid in the dispersal between suitable habitat. Additionally, Bell et al. (2017) showed that species traits modulate the species–area relationship, with small-bodied and flight capable carabid species on conifer-dominated lake islands in Saskatchewan (Canada) showing a negative species–area

TABLE 1 Generalised linear mixed model results (negative binomial models) testing for differences in the counts of species in three elytra length and wing form categories within each of the four habitat types investigated (Control forests, forest fragments in an agricultural landscape, an urban landscape and a lake landscape). Body size (elytra length) was categorised as small (0–5 mm, in the intercept), medium (>5–10 mm) and large (> 10 mm), while wing type was categorised as brachypterous (in the intercept), dimorphic and macropterous.

Elytra length	Coefficient (SE)	*p*	Wings	Coefficient (SE)	*p*
Control			Control		
Intercept	1.674 (0.234)	<0.001	Intercept	1.792 (0.209)	<0.001
Medium	−0.375 (0.385)	0.331	Dimorphic	−0.588 (0.350)	0.093
Large	−0.375 (0.355)	0.291	Macropterous	−0.588 (0.343)	0.086
Agriculture			Agriculture		
Intercept	1.459 (0.153)	<0.001	Intercept	1.629 (0.139)	<0.001
Medium	0.045 (0.214)	0.832	Dimorphic	−0.754 (0.244)	0.002
Large	−0.235 (0.229)	0.306	Macropterous	−0.082 (0.201)	0.685
Urban			Urban		
Intercept	1.634 (0.150)	<0.001	Intercept	0.865 (0.229)	<0.001
Medium	−0.456 (0.239)	0.057	Dimorphic	0.388 (0.300)	0.197
Large	−1.075 (0.302)	<0.001	Macropterous	0.582 (0.287)	0.042
Lake			Lake		
Intercept	1.145 (0.212)	<0.001	Intercept	0.452 (0.291)	0.121
Medium	−0.452 (0.342)	0.186	Dimorphic	0.167 (0.399)	0.676
Large	−1.299 (0.450)	0.004	Macropterous	0.493 (0.372)	0.185

relationship. In other words, small-sized species and those capable of flight are dominant on small islands. This is also the case in our study, where lake islands were generally small, and dominated by small species and those capable of flight. These small islands may not have sufficient resources for larger carabid species to survive and/or for flightless species to immigrate to, except via occasional drift (Bell et al., 2017; Kotze & Niemelä, 2002).

Carabid beetle assemblages in the fragments differed clearly between the different landscapes, both at the taxonomic level (NMDS results) and in terms of their trait distribution. Urbanisation appears to have a homogenising effect (see McKinney, 2006) on the beetles, more so than the agricultural or lake island landscapes, as shown by the lower variance between city fragments in the ordination. Our results support several studies on the taxonomic homogenisation of cities on insect taxa (Knop, 2016; Piano et al., 2017; Piano et al., 2020), but also contradicts previous studies on carabid beetles that emphasise the importance of local effects (Magura et al., 2010). Various interacting mechanisms can be responsible for differences in community structure between landscapes, ranging from light pollution in the city compared to other landscapes to differences in chemical pollution and pesticide types (insecticides and other pesticides in agricultural landscapes vs. heavy metals in the city [Halfwerk & Slabbekoorn, 2015; Botías et al., 2017; Forister et al., 2019; Eggleton, 2020]). In addition, a more constant heat-island effect in the city versus variable temperatures in other landscapes (Lövei & Magura, 2022; Manoli et al., 2019) and higher soil compaction and human use in urban forests (but also on lake islands during the summer) compared to forest patches in other landscapes (Grandchamp et al., 2000; Hamberg et al., 2008; Kotze et al., 2012) likely play a role. Control forests were utmost similar in their carabid assembly, and different from forest patches in the other landscapes, primarily because of their low species richness, and their dominance of generalist (64% of the number of individuals) and forest-associated individuals (36%) with no open-habitat species collected. In contrast, fragments in the urban and agricultural landscapes are dominated by generalist individuals (75%–79%), but with considerably fewer forest-associated (20%–22%) and some open habitat (1%–3%) individuals (Appendix S1, Table S1). In general, the trait–environment analysis can be summarised as follows; control forests are, expectedly, large and are associated with high percentages of OM and soil moisture, and subsequently with carabid traits that signal moisture affinity, intolerance to human environments and more short-winged species. Forest in the agricultural landscape are dominated by generalists, both in terms of habitat association, feeding preference and specialisation level. Agricultural lands can be quite homogenous spatially, but also extremely heterogeneous across years due to crop rotation. Such unpredictability in resources is likely to benefit organisms with a generalist lifestyle (Futuyama & Moreno, 1988; Krasnov et al., 2006). As mentioned above, urban fragments are dominated by generalist individuals of species tolerant of human environments and associated with dry habitats. Franzén et al. (2020) showed that moth communities consisted of multidimensional generalist species, supporting our results for carabid beetles in forests in urban and agricultural landscapes. For species to thrive in fragments in highly disturbed landscapes, it appears that a cocktail of traits at the generalist side of the trait spectrum increases the likelihood of these organisms to occupy disturbed environments. Finally, lake islands are typified by an abundance of ants, with carabid beetles capable of flight

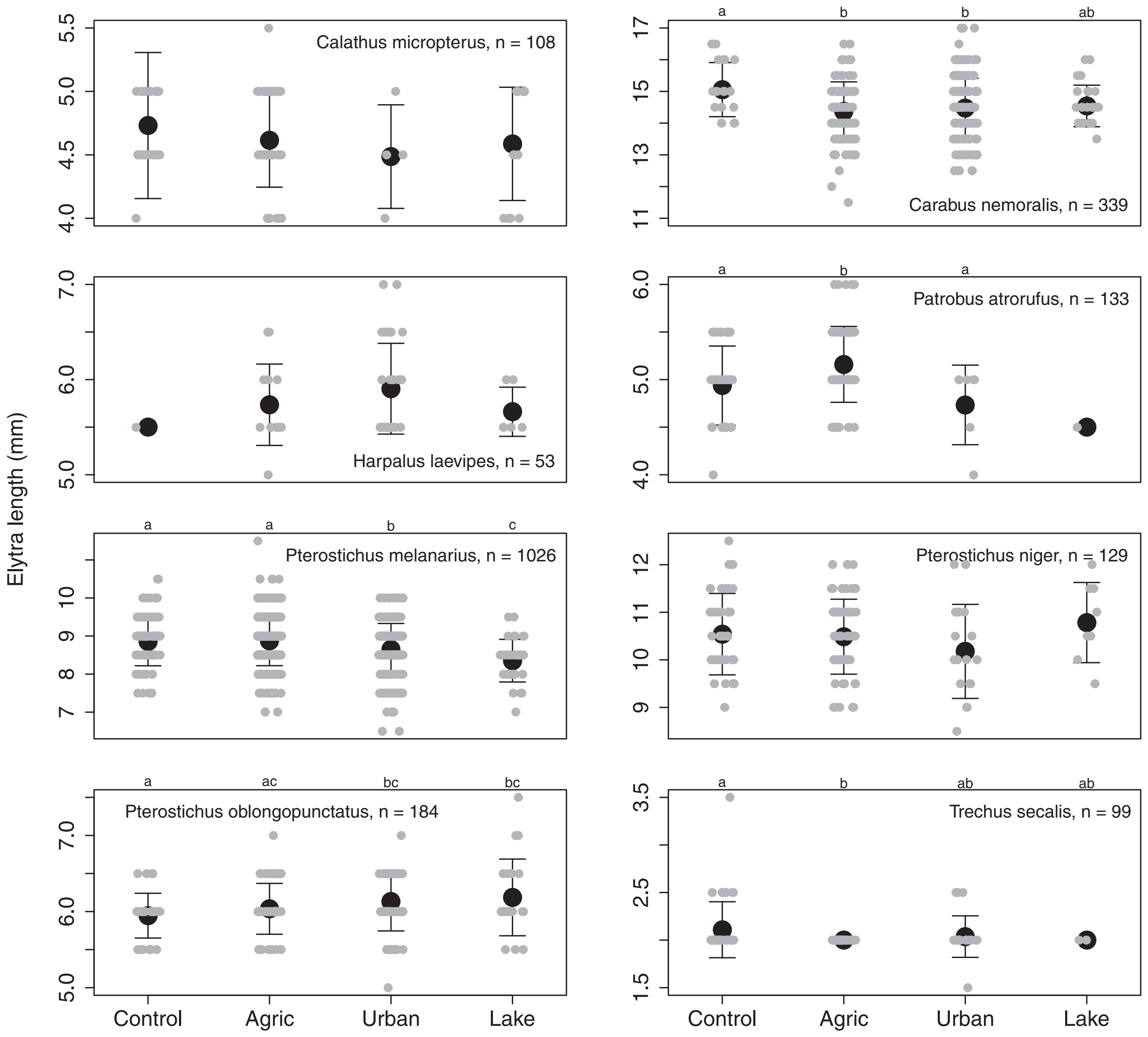


FIGURE 5 Body size (elytra lengths in mm) variation of eight abundant carabid species collected in forest fragments across the four landscapes investigated (control forests, agricultural, urban and lake landscapes). Data shown include geometric means, standard deviations and individual elytra lengths (grey dots). The number of individuals collected per species is also shown in each panel. See Table 2 for GLM test results. Different letters above the panels indicate significant differences between fragment types.

and a preference of granivorous species. Dispersal capacity is an important trait for insular communities, especially on true islands where the matrix can be instantly deadly. But once on the lake island, it appears that resource availability (see below) is of utmost importance, with our study favouring granivorous species rather than predators who are dependent on prey items that might be lacking.

Focusing specifically on body size and wing form, we show clear results. In terms of body size, our results support various studies that show an increased proportion of small-sized species at the community level with urbanisation (Fournier et al., 2020; Hahs et al., 2023; Merckx et al., 2018; Niemelä & Kotze, 2009), yet sometimes only so for forest specialists (Magura et al., 2020). Additionally, we show a decrease in the number of large species on lake islands, which both confirm (Dutch polder islands, Ranta & Ås, 1982) and contradict (Baltic Sea islands, Kotze & Niemelä, 2002) studies on these types of islands. Interestingly, in fragments of the agricultural landscape, the count of small-, medium- and large-sized species stayed roughly the same. A potential reason for the dominance of small species in urban fragments and in fragments on islands—but not in the agricultural landscape—is resource availability and quality, both within these patches and in the surrounding matrix (see discussion above on supplemental resources provided by the agricultural matrix). Recreational use of urban forests as well as lake island forests can have a considerable effect on soil properties, including compaction via trampling,

TABLE 2 GLM results (Gaussian models) testing the difference in elytra length of individual species within the forest fragments across the four landscapes investigated (Control forests [in the intercept], forest fragments in an agricultural landscape, an urban landscape and a lake landscape). Additionally, a Leven's test was performed to test for homogeneity of variances between the four landscapes investigated. A significant value indicates differences in variances between landscapes.

	Coefficient (SE)	*p*		Coefficient (SE)	*p*
Calathus micropterus[a]			*Carabus nemoralis*		
Intercept	1.554 (0.163)	<0.001	Intercept	15.079 (0.210)	<0.001
Agriculture	−0.025 (0.020)	0.219	Agriculture	−0.676 (0.227)	0.003
Urban	−0.053 (0.048)	0.272	Urban	−0.576 (0.220)	0.009
Lake	−0.031 (0.029)	0.290	Lake	−0.523 (0.274)	0.057
Levene's test	$F=0.352$	0.788	Levene's test	$F=1.563$	0.198
Harpalus laevipes[b]			*Patrobus atrorufus*[c]		
Intercept (Agric)	1.747 (0.020)	<0.001	Intercept	4.955 (0.061)	<0.001
Urban	0.029 (0.024)	0.231	Agriculture	0.220 (0.076)	0.004
Lake	−0.013 (0.036)	0.724	Urban	−0.205 (0.176)	0.248
Leven's test	$F=1.442$	0.246	Leven's test	$F=0.150$	0.861
Pterostichus melanarius			*Pterostichus niger*		
Intercept	8.882 (0.060)	<0.001	Intercept	10.573 (0.132)	<0.001
Agriculture	0.018 (0.066)	0.790	Agriculture	−0.057 (0.169)	0.735
Urban	−0.206 (0.071)	0.004	Urban	−0.351 (0.238)	0.143
Lake	−0.511 (0.127)	<0.001	Lake	0.239 (0.326)	0.464
Leven's test	$F=0.777$	0.507	Leven's test	$F=0.465$	0.707
Pterostichus oblongopunctatus			*Trechus secalis*		
Intercept	5.953 (0.066)	<0.001	Intercept	2.125 (0.034)	<0.001
Agriculture	0.092 (0.083)	0.270	Agriculture	−0.125 (0.050)	0.015
Urban	0.191 (0.079)	0.017	Urban	−0.077 (0.058)	0.186
Lake	0.251 (0.103)	0.016	Lake	−0.125 (0.156)	0.426
Leven's test	$F=2.953$	0.034	Leven's test	$F=2.299$	0.083

[a] Log transformed.

[b] Log transformed and without the control landscape since only one individual was collected from these control forests.

[c] Without the lake landscape since only one individual was collected from all lake islands.

which may affect larger species disproportionately compared to smaller ones. Carabid beetle larvae are soil bound and less mobile than adults, and large-bodied species usually have longer lasting life cycles than smaller bodied species, thus being more sensitive to soil disturbances (Blake et al., 1994). In addition, larger species generally have lower reproductive rates (Simberloff, 1994), making them more vulnerable to repeatedly disturbed environments. To summarise, the distribution and abundance of critical resources (e.g. prey, microclimate, shelter) are likely to affect large-bodied species more so than smaller species due to disturbances and simplification of these urban (see Gaston & Evans, 2010; Norton, 2011), and possibly lake island, forest fragments. Such habitat simplification does not necessarily occur in fragments in the agricultural landscape since people do not often visit these distant forest patches.

Not surprisingly, both urban and lake island communities are characterised by flight capable species (see also Hahs et al., 2023; Niemelä & Kotze, 2009; Piano et al., 2017; Zalewski & Ulrich, 2006). Dispersal ability is a key trait in the structuring of populations and communities (Dieckmann et al., 1999), and it is expected that the fragmented and isolated nature of forests in the urban environment and on lake islands filter carabid beetle communities based on the dispersal capacity of species. Similar to the patterns regarding body size, these two landscapes also experience frequent human and natural disturbances, a process that favours flight capable species (Venn, 2016), while stable habitats—the control forests in our case—favour brachyptery (Roff, 1990).

Overall, the urban and lake island matrices filter carabid beetle communities towards smaller species and species capable of flight, suggesting ecologically highly isolated forest fragments in these landscapes, and potential resource limitation. Since flightless species are generally larger in our study (mean brachypterous and macropterous elytra lengths: 8.26 mm (1.66 SE); 5.35 mm (0.41 SE), respectively), it seems that the fragmented nature of urban and lake landscapes is not optimal to their survival, both in terms of dispersing across inhospitable matrices and in terms of resource availability—these fragments are small and disturbed, and may thus not support larger sized species that typically are lower in abundance (Blackburn et al., 1993; White et al., 2007). Response to the agricultural landscape is different with no difference in size categories or in the count of flight capable versus flightless species. This is possible because of the benign to positive effect of the agricultural matrix in providing supplementary resources to beetles in the forests and in a less inhospitable matrix in terms of dispersal.

4.2 | Intraspecific variation in body size

Apart from the different numbers of large- versus small-sized species within carabid beetle communities in forest fragments surrounded by different landscape matrices, we also showed that individuals of the same species differ significantly in body size in forests embedded in different matrices. Similar to Weller and Ganzhorn (2004), we showed a significant decrease in body size of the large *Carabus nemoralis* in urban forest, but in our study also in agricultural forests. The most common species collected in our study, the medium-sized *Pterostichus melanarius* was also significantly smaller in urban (see also Sukhodolskaya, 2014) and lake island forests, but not in agricultural land forests. Both species are generalists of drier habitats (Lindroth, 1985, 1986) and are primarily flightless even though *P. melanarius* occasionally have individuals with long wings. Given their high numbers and generalist habit, it is likely that gene flow does occur between *P. melanarius* populations, which suggests that mechanisms other than genetic isolation may be more responsible for the decrease in body size. For instance, habitat quality in terms of the availability of resources and shelter in these urban, and lake island forests—and to some degree in the agricultural landscape—may affect larval development, likely expressed as smaller adults. Additionally, urban forests experience warmer, and drier, climatic conditions due to the urban heat island effect (Manoli et al., 2019), resulting in smaller adults as is evident in both laboratory experiments (see Koch et al., 2020; Tseng et al., 2018) and long-term insect collections (Tseng et al., 2018). Yet, it may also be that a slightly higher temperature at the time of reproduction can increase net reproduction, as was shown for the carabid species *Carabus auronitens* in the Westphalian lowlands in Germany (Niehues, Hockmann & Weber, 1996).

The consequences of a smaller body size are complex, and can be considerable. For instance, it is likely that smaller females will produce fewer eggs (but see above), or possibly smaller eggs of lower quality (Berger et al., 2008; Fox, 1994; Honěk, 1993). For whatever reason for smaller individuals in a stressed environment, consequences at the population level are at least twofold. First, a smaller female may produce fewer eggs but of the same size as a larger female. This will affect future population size negatively, possibly leading to inbreeding, genetically more depauperate populations (Kelemen & Rehan, 2021) and/or local extirpation. Second, females in isolated and small habitat patches may produce smaller eggs, which will result in smaller adults in future generations. Interestingly, a study on a forest specialist carabid (*Carabus convexus*) in and near the Hungarian city of Debrecen showed that urban females had significantly higher numbers of eggs than rural females, but that the urban population is still five times lower in abundance than its rural counterpart, possibly because of stressful environmental conditions for larval development in the city (Magura et al., 2021). The plasticity of this trait (body size and the quantity/quality of eggs produced) will determine the future makeup of populations. For instance, Bolnick et al. (2011) listed six general mechanisms by which trait variation can change the outcome of ecological interactions and can affect equilibrium densities, population stability and species coexistence. Body size is a fundamental trait linked to various other traits such as metabolic rate and life-history traits, including fecundity and longevity (Brown et al., 2004; Chown & Gaston, 2010): a change in intraspecific body size in a particular habitat is likely to have population-level consequences.

5 | CONCLUSIONS

We showed that the type of matrix surrounding indigenous spruce-dominated forest fragments in the boreal landscape affected carabid beetles within these forests, both at the community and intraspecific levels. Forest fragments in the city and on lake islands showed clear and expected effects, filtering the community towards smaller species and those capable of flight. Forest fragments in the agricultural landscape were species richer and did not show a clear response to the matrix in terms of body size and wing morphology changes, possibly due to the supplemental nature of resources from agricultural lands, and less disturbance in these forests as they are not visited frequently when compared to forests in the urban and on lake islands. It is also likely that natural habitat is available more so in the agricultural landscape compared to the other landscapes investigated, which has been shown to mitigate the loss of insect biodiversity worldwide, but only in low-intensity agricultural systems (Outhwaite et al., 2022).

We present clear evidence that the body sizes of a number of abundantly collected carabid species are changing significantly in the fragmented Boreal forest landscape. Beetles are primarily becoming smaller in these fragments compared to the large control forests. Such changes in morphology will have population-level consequences, yet it is unclear what drives these changes. At least in the urban environment, temperatures are higher (even within these forests, Kotze, unpublished results) which are likely to elevate metabolic rates of these ectotherms and consequently affect resource use and allocation, thus resulting in trade-offs between basal metabolism, growth and reproductive output (Sheridan & Bickford, 2011). A future step in our understanding of the effects of human-caused habitat fragmentation across a plethora of landscapes is to investigate the interplay between morphological and physiological traits, and whether the patterns we observe has a genetic basis.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The coordinates of all sites are presented as a footnote in Appendix S1, Table S1 and in Google Maps (https://www.google.com/maps/d/viewer?mid=1yfXKDPNiAPZTb5pAeLI8pkcMRMhXU-QN&ll=60.97618402244856%2C25.622075702995062&z=10). All species collected per site, including their traits and abundances are presented in Appendix S1, Table S1, while the detailed raw data are available here: DOI 10.5281/zenodo.8236387.

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BIOSKETCH

Johan Kotze is interested in the ecology or urban environments, primarily focusing on the responses of carabid beetles and plants to urbanisation, and in the ecosystem services provided by urban soils. This work was initiated by summer internships of two students (Matic Gabor and Sébastien Kohout) to our research group (Urban Ecosystem Research Group: https://www.helsinki.fi/en/researchgroups/urban-ecosystems).

Author Contributions: DJK and HS conceived the idea and led the writing. All authors collected the data, while MG and SK identified the beetles, contributed to the writing of the manuscript. DJK analysed the data.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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