The matrix affects carabid beetle assemblages in linear urban ruderal habitats

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Abstract

Matrix contrasts affect communities in patchy landscapes by influencing resources, abiotic conditions and spill-over effects. However, current knowledge is significantly biased towards forest and rural communities. We examined the effects of three different matrix types, i.e., low, intermediate and high contrasts, on carabid beetle assemblages at urban railway verges in two climatic regions. Study sites were located in Finland and in Slovenia. Using pitfall trapping, non-metric multidimensional scaling and generalised linear mixed models, we investigated carabid assemblages at railway verges and in differently contrasting adjacent matrices, i.e. built-up, grassland and forest. The matrix influenced carabid assemblages at railway verges. Assemblages grouped with adjacent matrix types, although some Finnish railway assemblages included a characteristic set of open dry habitat species. Abundances of generalist species at railway verges were higher when next to grassland or forest than urban matrices. Habitat specialists responded negatively to high contrast matrices, resulting in lower abundances of open habitat specialists in railway verges when next to forests and nearly no spill-over of forest specialists into railway verges. These patterns were consistent in both countries, i.e. irrespective of climatic region. Our study emphasises effects of the adjacent matrix and matrix contrasts on communities in linear open habitat patches in cities. Knowledge on matrix effects in patchy landscapes, such as urban environments, is essential in understanding the distribution and composition of communities in discrete patches. This knowledge can be used in conservation planning. If habitat specialists are negatively affected by high matrix contrasts, high contrasts should be avoided.

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Introduction

Communities in small habitat patches are exposed to matrix effects. For example, predation and competition are more intensive in small patches due to the spill-over of predators and competitors from matrices and the tendency of some animals to move along edges (Polis et al. 1997; Winter et al. 2000; Ries and Fagan 2003; Rand and Louda 2006; Schneider et al. 2012). Furthermore, the surrounding matrix isolates patches (Ricketts 2001), alters abiotic conditions within the patch or at least at the edges (Chen et al. 1995; Ries et al. 2004) and thus influences community composition within a habitat patch. To understand the community assembly processes in patchy landscapes, the mechanisms and role of matrix effects need to be investigated. Urban areas provide an excellent opportunity to investigate the effects of the matrix on habitat patches with a low interior-to-edge ratio (Luck and Wu 2002; Hamberg et al. 2009), such as railway verges. Here we investigated the effects of different matrix types (built-up, grassland and forest) on carabid beetle assemblages at railway verges in an urban setting in both cold (Finland) and warm temperate climatic regions (Slovenia) (Lomolino et al. 2010).

The presence of a species in a patch can be affected by matrix contrast, which is the magnitude of difference in ecologically meaningful features (e.g. vegetation height and density, microclimate) between the focal patch and the surrounding matrix. As such, it is related to edge contrast and includes edge effects (see Wiens et al. 1993; Harper et al. 2005) but the emphasis is on the effects of the matrix on within-patch processes. Matrix contrasts are thought to affect the strength of edge responses, i.e. a higher contrast results in an edge response of higher magnitude (Ries et al. 2004; Harper et al. 2005). For example, forest carabid beetles avoid edges with high contrast matrices more than with low contrast matrices (Noreika and Kotze 2012), and similar patterns have been observed for other habitat specialist taxa (DeGraaf and Yamasaki 2002; Reino et al. 2009; Campbell et al. 2011). Consequently, these species can be absent from small patches with high contrast matrices. In contrast, habitat generalists are usually not influenced by the perceived edges or even benefit from the adjacency of a contrasting matrix (Fagan et al. 1999; Ries and Debinski 2001; Gaublomme et al. 2008; Reino et al. 2009; Noreika and Kotze 2012; Peyras et al. 2013). However, rigorous studies on this topic are rare (Ries et al. 2004; Ries and Sisk 2008).

Ries and Sisk (2004; 2008) suggested that distribution patterns of organisms at edges and in habitat patches reflect the distribution of resources (e.g. food, nesting sites) and abiotic conditions. However, resource availability and abiotic conditions are also affected by the matrix contrast. In particular, abiotic conditions (e.g. temperature, insolation and humidity) within small patches are rather similar to the adjacent matrix (Chen et al. 1995; Cadenasso et al. 1997; Delgado et al. 2007), resulting in subsequent changes in the biota within the patch (Murcia 1995; Fagan et al. 1999; Harper et al. 2005). Additionally, matrix contrast controls the flow of organisms from the matrix to the patch by influencing their reluctance of entering the patch. Novel or intensified interactions caused by the flow of matrix organisms can suppress or subsidize some species within habitat patches (Polis et al. 1997; Fagan et al. 1999; Tscharntke et al. 2005).

Our knowledge about the effects of matrix contrasts on open habitat communities is limited, as the predominant research focus has been on forests (e.g. Reino et al. 2009; Lacasella et al. 2015). Urban communities, representing taxa living in disturbed and often open habitat types, likely respond less acutely to adjacent matrices, as they could be adapted to living in small patches (Harper et al. 2005). Communities in cities have higher proportions of generalist species and lower proportions of strict habitat specialists (e.g. Elek and Lövei 2007; Gaublomme et al. 2008; Niemelä and Kotze 2009), which should cause weak responses of communities to adjacent matrices. On the other hand, at least forest species and communities respond strongly to habitat edges, and especially to high contrast matrices (Gaublomme et al. 2008; Brearley et al. 2010; Noreika and Kotze 2012). Linear strips of open habitat in the urban environment, such as ruderal vegetation strips along railway tracks, provide an excellent opportunity to test the role of contrasting matrices (built-up, grassland and forest) on communities of open habitat species within these rather homogenous verges. Particularly, verges host dry open habitat specialists that are able to exploit this novel habitat (Vermeulen 1993; Eversham and Telfer 1994; Eversham et al. 1996; Koivula et al. 2005; Noordijk et al. 2008).

Our aim was to examine how carabid beetle assemblages living in a linear ruderal habitat (railway verge) are influenced by surrounding matrices of different levels of contrasts. Hence, we investigated the structure of carabid beetle assemblages in Finland and Slovenia at railway verges and in the adjacent low, intermediate and high contrast matrices, or built-up, grassland and forest, respectively. Carabids are useful as model organisms, as traits of most carabid species are well known, and landscape features affect their spatial distribution and population dynamics (Lövei and Sunderland 1996; Kotze et al. 2011). Our hypotheses are that: (i) railway verge carabid assemblages share characteristics with their respective matrix type due to strong matrix effects in linear habitats (Ewers and Didham 2006). However, the harshness of these linear strips may, alternatively, result in unique carabid beetle communities in these strips irrespective of the adjacent matrix habitat; and (ii) the activity densities (hereafter abundances) of habitat specialists are negatively affected by high contrast matrices (e.g. DeGraaf and Yamasaki 2002; Noreika and Kotze 2012), while (iii) generalists are more abundant at railway verges adjacent to grasslands and forests due to more favourable conditions resulting from altered abiotic conditions and spill-over effects (Polis et al. 1997; Tscharntke et al. 2005; Rand and Louda 2006; Schneider et al. 2013). Finally, we evaluate whether the responses of carabid beetle species and communities are consistent in the two climatic regions investigated.

Material and methods

Study areas

Study sites were located in the cold climatic region in Helsinki and Lahti, Finland (60°12'–60°58' N, 24°44'–25°41' E), and in the warm temperate climatic region in Ljubljana, Slovenia (46°1'–46°6' N, 14°26'–14°34' E) (Lomolino et al. 2010). Both Finland and Slovenia have similar land uses in these areas: forest cover over 60%, cropland cover below 15%, and grassland cover about 10% in Finland and 21% in Slovenia (Eurostat 2012). The similar land use allows comparing results more readily. We collected carabid beetle assemblages in narrow verges of actively-used railways and in adjacent matrices (built-up, grassland or forest). The three treatments (i.e. railway verge – matrix pairs) represented differing matrix contrasts: 1) low (railway–built-up), 2) intermediate (railway–grassland) and 3) high (railway–forest). Four replicates were chosen for each treatment, resulting in 12 study sites per country. The adjacent matrix habitats were at least 1 ha in size to ensure that these matrix habitats have characteristic carabid beetle assemblages (Mader 1984). The minimum distance between individual study sites was 800 m. Railway verges were narrow with mean widths being 4.2 m (SD = 2.3) in Finland and 2.0 m (SD = 1.4) in Slovenia.

In both countries, verges featured a dry microclimate, mostly ruderal sparse vegetation and gravelly or somewhat sandy topsoil. The verges are occasionally treated with herbicide or mown to keep the vegetation low. The adjacent matrix affected the vegetation, as it was denser close to intermediate and high contrast matrices and some species of the adjacent habitat were present, such as small tree saplings. The built-up matrix was largely covered by gravel and asphalt and had very sparse vegetation. In contrast to extremely dry conditions at the built-up matrix, grasslands had a dense grassy vegetation. All forest patches in Finland were mesic and dominated by mature Norway spruce trees (*Picea abies*), while forest patches in Slovenia were predominantly deciduous stands of pedunculate oak (*Quercus robur*) and common hornbeam (*Carpinus betulus*) or hybrid poplar (*Populus* X *canadensis*) or common alder (*Alnus glutionosa*).

Carabid beetle sampling

Carabid beetles (Coleoptera, Carabidae) were continuously sampled by pitfall trapping in 2013 from May to October (Finland) or November (Slovenia). The sites were visited and the samples collected every 2-3 weeks in Finland and due to logistic reasons, 2-7 weeks in Slovenia (2-4 weeks at the peak of carabid activity), resulting in five visits per country. Ten traps were installed at each site (totalling 120 traps per country) in two trap lines: 1) five traps were placed in the verge near or occasionally into ballast rocks of the railway track depending on the verge size, and 2) another five traps in the adjacent matrix at 20-30 m from the railway verge trap line, to sample the assemblage immediately adjacent to the verge. The distance between traps within a trap line was 5 m. The catch of the five traps per trap line was pooled per visit. In Finland, 14 traps were lost (2.3% loss) compared to 94 traps (15.7% loss) in Slovenia. Traps were considered “lost” if they were flooded, filled with bycatch such as snails or had simply vanished. The lost traps and unequal sampling effort were accounted for in the statistical analyses (see below).

The traps - plastic cups - were dug into the ground with their rim flush with the ground surface. Half the cup was filled with a 50% propylene glycol-aqueous solution to kill and preserve the invertebrates. In Finland, the mouth diameter and volume of the traps were 65 mm and 250 ml, and dark plastic roofs (10 x 10 cm) were installed approximately 2 cm above each cup to prevent rain, debris and small mammals from entering the traps. In Slovenia, traps with mouth diameter of 100 mm and volume of 500 ml were used, and tree bark was used as a roof. The collected invertebrates were taken to the laboratory and preserved in denatured ethanol. All adult carabid beetles were identified to species level where possible, and their habitat associations were recorded by using the keys of Lindroth (1985; 1986) and Luff (2008) in Finland, and Müller (1930/31) and Müller-Motzfeld (2006) in Slovenia.

Environmental variables

A set of environmental variables was recorded to describe habitat conditions at the sites. Percentage covers (scale: 0, 5, 10, …., 100%) of ground-layer vegetation (herb, grass and moss), shrubs, litter, bare soil and rock were estimated visually from photos taken in the end of July in Slovenia and in the beginning of August in Finland, from a 1 x 1 m quadrat around each pitfall trap, and averaged per trap line.

Soil samples were taken from 0-10 cm depth near each trap during two consecutive days to measure soil pH, soil moisture (%) and organic matter content (%). Soil pH was measured using a WTW inoLab pH/Cond 720 meter from a suspension of soil and distilled water (ratio 1:3, volume). Soil moisture content was determined by drying the soil in an oven: 20 g of soil was placed into an oven for 24 h at 70°C and then weighted again after cooling in a desiccator. Organic matter (i.e. loss on ignition) in dried samples was burnt in a muffle oven at 550°C for 5 h and weighted after cooling in a desiccator. Subsequently, moisture and organic matter content were calculated using the obtained masses. Soil pH, moisture and organic matter content were then averaged per trap line. Soil organic matter was later removed from the analyses as tests revealed strong correlations with several environmental variables and especially with soil moisture (r_s = -0.779, $p < 0.001$ for Finland and r_s = 0.833, $p < 0.001$ for Slovenia). In the Slovenian data, soil moisture (%) was negatively correlated with soil pH (r_s = -0.834, $p < 0.001$) and a few variables were correlated in the Finnish data, but these were retained in the non-metric multidimensional scaling analyses (see below) due to potentially independent and likely important effects. Particularly, bare soil cover (%) was negatively correlated with soil moisture (%) (r_s = -0.892, $p < 0.001$) and degree of urbanisation with soil pH (r_s = 0.724, $p > 0.001$) in the Finnish data.

To further assess habitat quality, several additional variables were recorded. The width of the railway verge was measured from the ballast rocks of a railway track to the edge of the adjacent matrix (i.e. markedly different in vegetation structure and height) at the first, third and fifth trap in the trap line, and averaged per site. In addition, distance between the railway trap line and the matrix trap line was measured per site. An approximate value for slope (in degrees) was measured at the trap line for verge and matrix at each site. To measure the degree of urbanisation for Finland, imperviousness within a 500 m buffer around each study site was assessed using ArcGIS for Desktop (Esri 2014) and base maps from the National Land Survey for Finland (2009). For Slovenia, percentage of area classified as “urbanised and other similar lands” from the Land Use Map RABA (2012) within a 500 m buffer was used as the degree of urbanisation.

Statisticl analyses

Non-metric multidimensional scaling (NMDS) was used to investigate the effects of the adjacent matrix on carabid beetle assemblage structure among the three treatments for Finland and Slovenia separately. The environmental variables mentioned above were used in these ordinations. The analysis was performed in R (R Core Team 2013), using the vegan package (Oksanen et al. 2013). The number of carabid individuals was standardized to 100 trapping days to correct for lost traps and unequal sampling effort. The Bray-Curtis coefficent was used as a dissimilarity measure in the three-dimensional ordination calculation; dimensions 1 and 2 were plotted. The envit function in the vegan package was used to evaluate the significance of environmental variables in these ordinations.

Generalised linear mixed models (GLMMs) were run in R (R Core Team 2013) to investigate the impacts of adjacent matrices on carabid beetle abundances at the railway verges. The most abundant species (with more than 33 individuals collected) were analysed individually, while the less abundant species were analysed after being pooled into groups based on associated habitat and moisture affinities obtained from the local keys (see above) [dry open habitat (OD), open habitat generalist (OG), moist open habitat (OM), dry habitat generalist (GD), habitat generalist (G), moist habitat generalist (GM), dry forest (FD), forest generalist (F) and moist forest (FM)]. Models simply did not work or returned unrealistic coefficients and standard errors when species fewer than 33 individuals captured were analysed, presumably due to the clumped nature or abundance data. Also abundant species with highly clumped data were excluded from the analyses (Online Resource 1). Further, forest species were not analysed with GLMMs, since these species only occurred in the railway–forest treatment. The glmer function in the lme4 package (Bates et al. 2014) was used for the analysis. The response variable (i.e. number of carabid individuals) was modeled following a Poisson distribution (O’Hara and Kotze 2010). To account for possible overdispersion in the response variable, an individual-level random effect was added (Harrison 2014).
Models included the following fixed effects: 1) collecting visit as a factor, 2) log number of trapping days as an offset term to account for trap losses (Kotze et al. 2012), 3) treatment as a factor (i.e. the three railway–matrix pairs), 4) trap line as a factor, 5) the treatment × trap line interaction, 6) soil moisture, and 7) soil pH. In addition to the fixed effects in Finnish models, city (factor) was included as a random effect to account for possible impacts of different localities. In the Slovenian models, soil pH was removed due to its strong correlation with soil moisture. If a modeled species or species group was not, or rarely observed in a treatment, trap

line, city or during a visit, that particular component was removed from the analysis for that species or group. As such, some effects were excluded from the models, due to very low abundances there. Further, the interaction between treatment and trap line had to be removed for some species due to unsuitable outputs resulting from overly complex models. Lost traps and unequal sampling effort were accounted for by adding the first and second fixed effects (see above) to the models.

Results

In total, 59 carabid beetle species (1065 individuals) were collected in Finland and 70 species (3861 individuals) in Slovenia (Online Resource 1). The railway verge catch was dominated by dry open habitat species (18 species and 262 individuals in Finland, 21 species and 882 individuals in Slovenia), such as *Calathus erratus* (*n* = 122) and *Amara municipalis* (*n* = 69) in Finland, and *Harpalus rufipes* (*n* = 516) and *Harpalus honestus* (*n* = 117) in Slovenia.

Matrix effects on carabid beetle assemblages

NMDS ordinations primarily suggest that the matrix influences carabid beetle assemblages at railway verges, i.e. assemblages in the verges are grouped with their respective matrix type in both countries (Figs. 1a and 1b), yet high variation (i.e. scatter) was observed for assemblages in the railway–built-up treatment. In particular, the railway verge assemblages adjacent to forest matrices are associated with moist habitat species and generalists, while railway verge assemblages adjacent to grassland and built-up matrices are associated with dry habitat and generalist species (Online Resources 2 and 3). Even though the adjacent matrix had an effect on carabid beetle assemblages, in Finland (but not in Slovenia) the railway verge also seems to have a characteristic set of species, since a number of verge sites grouped together in the centre of the ordination (filled symbols in Fig. 1a) irrespective of matrix type.

Vector fitting revealed that in both countries carabid beetle assemblages were correlated with soil conditions (pH, soil moisture), percentage ground cover measures (bare soil, litter, and rock) and degree of urbanisation (% imperviousness or urbanised lands within a 500 m buffer) (Online Resource 4). The railway–forest treatment was associated with higher soil moisture content and litter cover, while the railway–built-up treatment was associated with higher rock and bare soil cover. In Slovenia, the railway–built-up treatment was also associated with higher urbanisation. Habitat conditions in the railway–grassland treatment were somewhat different in Finland compared to Slovenia. Despite both tending to be associated with intermediate conditions compared to the other treatments (Figs. 1a and 1b), assemblages in the railway–grassland treatment in Finland were associated with a higher cover of ground-layer vegetation, which did not correlate with any of the assemblages in Slovenia. The beetle-environment associations described above are reflected in habitat conditions at railway verges, which were generally moister and with higher litter cover adjacent to grasslands or forests in both countries (Online Resource 5).

Responses of individual species and species groups to the adjacent matrices

Impacts of the matrix on the abundances of individual carabid beetle species and species groups at railway verges varied, but was generally comparable among species of similar habitat affinity and among countries (Table 1, Figs. 2 and 3). In Finland, open dry habitat species (*Calathus erratus*, *Amara cursitans, A. municipalis*, Group OD) occurred almost exclusively in railway verges, thereby representing here “true” railway verge species. Abundances of these habitat specialists showed a positive trend towards the low contrast matrix (Table 1, Fig. 2). Forest specialists clearly showed sensitivity towards high contrast matrices, since virtually no forest specialist individuals were collected from railway verges adjacent to forests and were rarely collected in any of the other treatments (Online Resource 1). The abundances of habitat generalists [*Carabus nemoralis* (G), *Pterostichus niger* (GM), *Trechus secalis* (GM), and Groups GD, OG, G, GM] were generally highest at the railway–forest treatment, while lowest at the railway–built-up treatment (Table 1, Fig. 2). The preferred habitat (i.e. railway verge or matrix) for generalists within treatments varied without being clearly related to the species’ moisture affinities. Nevertheless, it was clear that the adjacency of grasslands and forests increased the abundance of generalists in railway verges.

In Slovenia, no habitat specialist species exclusively occurred in railway verges, although some open dry habitat species were rather frequently found (Fig. 3). As in Finland, *Amara* spp. occured almost exclusively in railway verges, but were considered as generalists in Slovenia since individual species could not be identified (Online Resource 1). The open dry habitat species in Slovenia (*Calathus fuscipes*, *C. melanocephalus*, *Harpalus affinis*, *H. rufipes*, Group OD) were generally associated with grasslands (Table 1, Fig. 3). While these species were present in railway verges irrespective of matrix type, the abundances of some species (*Harpalus rufipes*, Group OD) were higher next to grasslands. As in Finland, Slovenian forest specialists avoided railway verges (see Online Resource 1). Furthermore, generalists [*Amara* spp. (G), *Carabus coriaceus* (G), *Abax carinatus* (GM), *C. granulatus* (GM), and Groups OG, GM] followed an abundance pattern similar to Finland, although abundances in the railway verges were generally markedly lower compared to the matrix (Table 1, Fig. 3). Notably, also *Amara* spp. benefited from the adjacency of grasslands and especially forests, despite occurring almost exclusively in railway verges.

Discussion

Our study demonstrated that the adjacent matrix type has a clear influence on carabid beetle assemblages at railway verges, stressing the impact of the matrix on communities in narrow, linear urban habitat patches (Ewers and Didham 2006; Fletcher et al. 2007), and likely in fragmented environments in general. Specifically, assemblages at railway verges adjacent to grasslands and especially to forests comprised proportionally more habitat generalists compared to assemblages adjacent to built-up matrices. In line with our second hypothesis, results also suggest a negative effect of high contrast matrices on habitat specialists, although this was clear only for forest species. In Finland, open dry habitat specialists followed the expected pattern, i.e. these species occurred abundantly in railway verges and were negatively affected by high contrast matrices. In Slovenia, open dry habitat specialists did not follow our expectation of high occurrence in railway verges, being generally scarce in verges and occurring abundantly in grasslands. However, abundances in railway verges were seldom higher adjacent to grasslands, indicating that these species occasionally spilled over from grasslands into the railway verge. The observed patterns of matrix effects were shown to be consistent irrespective of climatic region.

The effects of matrix contrast on habitat specialists

Similarly to forest species, many open habitat species are declining due to the intensifying pressures of agriculture, urbanisation and climate change (Stoate et al. 2009; Kotze et al. 2011; González-Varo et al. 2013). Our results suggest that open habitat specialists profit from railway verges if contrast with the matrix is low and other conditions are favourable. Both open habitat and forest specialists responded negatively to high contrast matrices, which is consistent with the observed change in habitat conditions at verges and the edge effect literature (e.g. DeGraaf and Yamasaki 2002; Koivula et al. 2004; Campbell et al. 2011; Lacasella et al. 2015). Further, habitat specialists appeared to respond less negatively to intermediate contrast matrices. While such a pattern has been reported before both for open habitat and forest species of, e.g. birds, carabid beetles and other insects (e.g. Reino et al. 2009; Noreika and Kotze 2012; Korpela et al. 2015), it contradicts with Ries and Debinski (2001), who noted that an open habitat butterfly species responded negatively to all matrices, irrespective of contrast. Ries and Sisk (2004, 2008) proposed that species simply respond to the amount of suitable resources. While this may be true to some extent, we argue that the matrix contrast, together with changes to the biotic and abiotic environment, affects how species respond across these gradients (see also Harper et al. 2005; Campbell et al. 2011).

Finnish railway verges hosted a characteristic set of open dry habitat specialists (of which only *Harpalus rufipes* was rather abundant in the Slovenian railway verges). This indicates that urban railway verges can be exploited by some open dry habitat specialists, perhaps adapted to these harsh conditions (Harper et al. 2005). Railway verges in Slovenia proved to be considerably poorer habitat for open habitat specialists compared to Slovenian grasslands and Finnish railway verges. This unexpected result can arise from the narrower verge width (Vermeulen 1995; Saarinen et al. 2005), higher soil pH (Paje and Mossakowski 1984), higher rock cover and lower vegetation cover (Brose 2003) compared to Finland (Online Resource 5). Species diversity and abundance within the railway verges could also reflect matrix variables we did not investigate, such as the amount of similar open habitats in the landscape (Vermeulen 1993; Lizée et al. 2011), which is lower in Finland (Eurostat 2012). Large variation within the railway–built-up treatment indicates high species turnover, common for disturbed habitats and cities (Rebele 1994).

The effect of different matrix types on generalists at railway verges

Edge response studies indicate that habitat generalists are usually not affected by perceived edges, but rather spill over into other habitats (Tscharntke et al. 2005; Noreika and Kotze 2012; Peyras et al. 2013). Considering the high abundance of habitat generalists in grasslands and forests, and similar patterns in railway verges, our results from both countries suggest spill-over. Additionally, it is possible that the diversity and abundances of generalists were favoured by the higher moisture, increased vegetation and litter cover adjacent to grasslands and forests, despite the fact that individual species were generally unresponsive to soil moisture. For example, increased litter cover and/or ground-layer vegetation can provide shelter and prey (e.g. Koivula et al. 1999). The consistent pattern of increasing abundances of generalists at railway verges adjacent to matrices with higher productivity can also be linked to higher influxes of resources (e.g. prey items) from the matrix (Polis et al. 1997; Ewers and Didham 2006).

Conclusions

Our study showed consistent effects of the matrix on carabid beetle communities in a narrow, linear urban habitat. Such habitats can be considered "all edge", where community structure depends on matrix contrast and on the abundance of generalists within adjacent habitats (see Sisk et al. 1997). Spill-over of habitat specialists from low contrast matrices and of generalists can increase species diversity in the verge. However, changes in environmental conditions at high contrast matrices create an "invisible barrier" for most habitat specialists within these habitats, diminishing their value as a habitat and potentially as a corridor. It is important to note that reducing matrix contrast can improve habitat conditions for these species, given that linear habitats, such as road and railway verges, and urban green corridors, are wide enough.

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Fig. 1 Non-metric multidimensional scaling ordinations of carabid beetle assemblages at the railway–matrix treatments (i.e. railway–built-up, railway–grassland and railway–forest) for a) Finland and b) Slovenia. The ellipses indicate 1 SD of the weighted average of site scores of the railway–built-up treatment (dotted line), the railway–grassland treatment (dashed line), and the railway–forest treatment (solid line). Abbreviations of the significant environmental vectors shown: rock = rock cover (%), litter = litter cover (%), soil.moist = soil moisture content (%), bare.soil = bare soil cover (%), urban = urbanisation degree (% of pavement/urbanised lands within a 500 m buffer), soil.ph = soil pH, g.l.vegetation = ground-layer vegetation cover (%)

Fig. 2 Predicted mean (± SE) abundances of Finnish individual carabid beetle species and species groups at three treatments (railway–built-up, railway–grassland, railway–forest). Abbreviations for habitat associations of the species and groups: OD = dry open habitat, G = habitat generalist, GM = moist habitat generalist

Fig. 3 Predicted mean (± SE) abundances of Slovenian individual carabid beetle species and species groups at three treatments (railway–built-up, railway–grassland, railway–forest). Abbreviations for habitat associations of the species and groups: OD = dry open habitat, G = habitat generalist, GM = moist habitat generalist

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Table 1 Generalised Linear Mixed Model results for carabid beetle species and species groups (data of less abundant species pooled; see Online Resource 1) of the railway–matrix treatments (i.e. railway–forest, railway–grassland, railway–built-up). The species and species groups were *a priori* listed from dryness associated (top) to moisture associated (bottom) for both Finland and Slovenia. Coefficients, standard errors (SE) and *p*-values are shown for intercepts, treatments (treatm.), matrix trap lines, soil moisture (%), soil pH, and the treatment x trap line interaction. Significant and near significant *p*-values are in boldface. Abbreviations for habitat associations: OD = dry open habitat, OG = open habitat generalist, OM = moist open habitat, GD = dry habitat generalist, G = habitat generalist, GM = moist habitat generalist, FD = dry forest and FM = moist forest

		Intercept [a]	Grassland treatm. (G)	Built-up treatm. (B)	Matrix trap line (M)	Soil moisture (%)	Soil pH	G x M	B x M
Finland									
Calathus	Coefficient	-9.283	1.730	-0.089		-6.884	-2.429		
erratus (OD)	(SE)	(2.269)	(1.194)	(1.351)		(2.345)	(0.841)		
	p-value	**< 0.001**	0.148	0.948		**0.003**	**0.004**		
Amara	Coefficient	-12.300		3.136		-2.855	-1.188		
cursitans (OD)	(SE)	(8.836)		(4.586)		(12.587)	(2.085)		
	p-value	0.164		0.494		0.821	0.569		
Amara	Coefficient	0.094			-3.988	12.405	1.810		
municipalis	(SE)	(6.118)			(1.729)	(8.127)	(1.486)		
(OD)	*p*-value	0.988			**0.021**	0.127	0.223		

Group OD	Coefficient	-6.151	1.632	0.139	-0.324	-1.088	0.578	-1.148	-0.008
	(SE)	(0.999)	(1.000)	(1.138)	(1.739)	(0.968)	(0.493)	(1.812)	(1.875)
	p-value	< **0.001**	0.102	0.903	0.852	0.261	0.241	0.526	0.996
Group GD	Coefficient	-5.764	0.703	-2.040	-2.510	1.225	1.270		
	(SE)	(0.754)	(0.767)	(1.257)	(0.713)	(0.285)	(0.494)		
	p-value	< **0.001**	0.359	0.105	< **0.001**	< **0.001**	**0.010**		
Group OG	Coefficient	-7.776	0.822	-0.377	1.713	-3.495	-0.065		
	(SE)	(1.072)	(0.840)	(0.911)	0.621	(1.101)	(0.460)		
	p-value	< **0.001**	0.327	0.679	**0.006**	**0.002**	0.887		
Carabus nemoralis (G)	Coefficient	-1.405	-3.992	-3.907	0.637	0.324	1.307	0.306	-4.581
	(SE)	(1.192)	(1.016)	(0.934)	(0.667)	(0.381)	(0.495)	(1.027)	(1.244)
	p-value	0.239	< **0.001**	< **0.001**	0.340	0.395	**0.008**	0.766	< **0.001**
Group G	Coefficient	-2.639	-1.947	-4.191	-0.871	0.236	1.028	1.766	-0.388
	(SE)	(0.580)	(0.741)	(1.123)	(0.781)	(0.384)	(0.488)	(0.910)	(1.580)
	p-value	< **0.001**	**0.009**	< **0.001**	0.265	0.538	**0.035**	**0.052**	0.806
Pterostichus niger (GM)	Coefficient	-3.954	-3.187	-1.515	-5.308	1.731	0.173	5.326	-4.638
	(SE)	(1.478)	(1.805)	(1.864)	(2.899)	(0.921)	(0.633)	(2.444)	(65.177)
	p-value	**0.007**	0.078	0.416	**0.067**	**0.060**	0.785	**0.029**	0.943
Trechus secalis (GM)	Coefficient	-4.999	-2.098		-1.411	1.282	0.052	2.271	
	(SE)	(0.846)	(1.146)		(1.040)	(0.464)	(0.634)	(1.272)	
	p-value	< **0.001**	**0.067**		0.175	**0.006**	0.935	0.074	

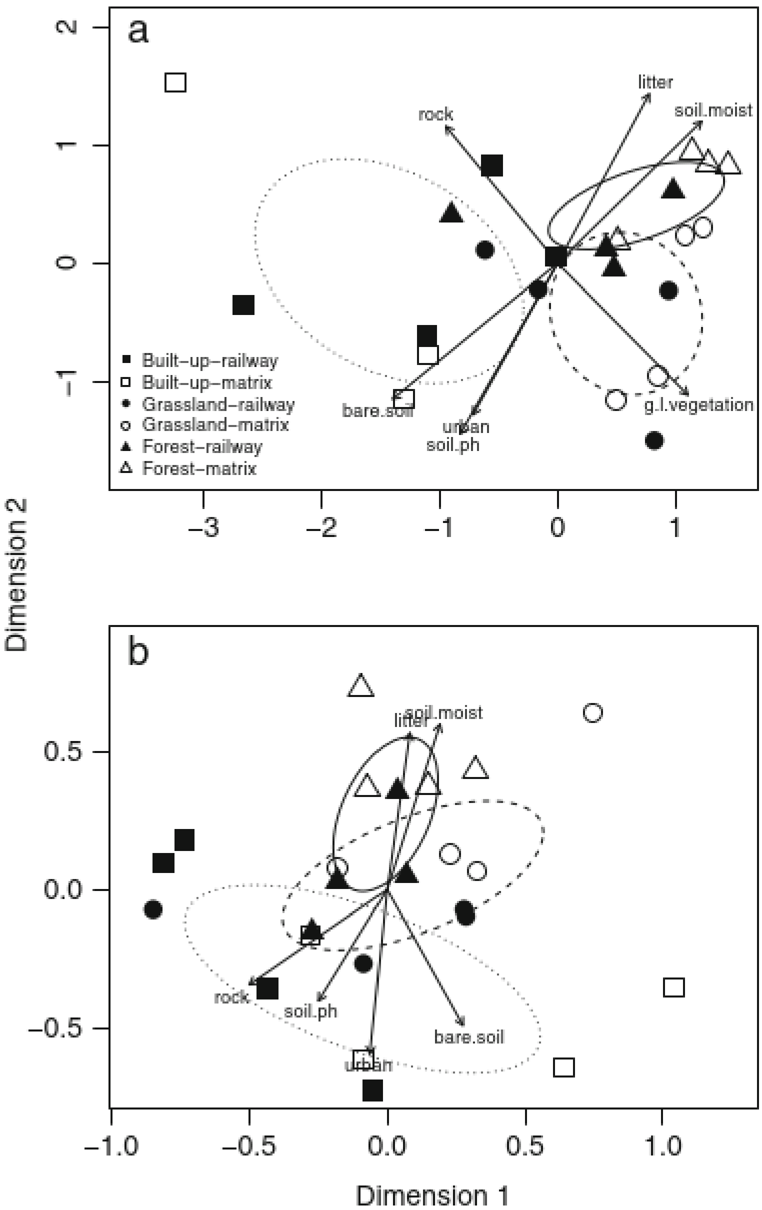
Group GM	Coefficient	-2.698	-2.645		-3.686	1.340	0.155	4.474	
	(SE)	(0.526)	(0.879)		(1.363)	(0.459)	(0.428)	(1.400)	
	p-value	< **0.001**	**0.003**		**0.007**	**0.004**	0.717	**0.001**	
Slovenia									
Harpalus affinis	Coefficient	-7.800		-0.242	2.165	-0.410			-1.580
(OD)	(SE)	(1.555)		(1.594)	(1.818)	(0.777)			(2.361)
	p-value	**<0.001**		0.879	0.234	0.598			0.503
Harpalus	Coefficient	-10.522	1.845	-0.721	-0.654	1.193			
rufipes (OD)	(SE)	(1.827)	(1.466)	(1.998)	(1.373)	(0.805)			
	p-value	**<0.001**	0.208	0.718	0.634	0.139			
Calathus	Coefficient	-10.839			2.119	3.864			
melanocephalus	(SE)	(2.478)			(1.427)	(2.643)			
(OD)	*p*-value	**<0.001**			0.138	0.144			
Group OD	Coefficient	-6.370	0.973	-0.894	-0.250	-0.627		1.209	2.848
	(SE)	(0.664)	(0.787)	(0.952)	(0.998)	(0.392)		(1.190)	(1.310)
	p-value	**<0.001**	0.217	0.348	0.802	0.110		0.310	**0.030**
Calathus	Coefficient	-9.590	2.348		0.921	0.258			
fuscipes (OD)	(SE)	(1.203)	(0.876)		(0.882)	(0.525)			
	p-value	**<0.001**	**0.007**		0.296	0.623			
Group OG	Coefficient	-8.261			0.213	0.054			
	(SE)	(2.518)			(2.101)	(1.061)			
	p-value	**0.001**			0.919	0.959			

Amara spp. (G)	Coefficient	-3.806	-0.657	-0.894		-0.164			
	(SE)	(0.618)	(0.761)	(0.796)		(0.329)			
	p-value	**<0.001**	0.388	0.262		0.619			
Carabus	Coefficient	-6.500	-1.819	-0.646	1.453	-0.190		-0.390	-2.480
coriaceus (G)	(SE)	(0.570)	(0.675)	(0.565)	(0.573)	(0.215)		(0.862)	(0.908)
	p-value	**<0.001**	**0.007**	0.253	**0.011**	0.379		0.651	**0.006**
Abax carinatus	Coefficient	-6.509	-0.809		1.159	0.224		0.456	
(GM)	(SE)	(0.648)	(0.942)		(0.716)	(0.262)		(1.077)	
	p-value	**<0.001**	0.390		0.106	0.393		0.672	
Carabus	Coefficient	-7.888	-0.929		1.101	0.614		0.317	
granulatus	(SE)	(1.303)	(1.696)		(1.411)	(0.564)		(2.044)	
(GM)	*p*-value	**<0.001**	0.584		0.436	0.276		0.877	
Group GM	Coefficient	-6.574	-0.437	-2.445	1.794	-0.190			
	(SE)	(0.599)	(0.498)	(0.796)	(0.569)	(0.275)			
	p-value	**<0.001**	0.380	**0.002**	**0.002**	0.491			

[a] The intercept for Finnish data represents the prediction at visit 1, railway–forest treatment and railway verge trap line where possible, i.e. for Group OD, Group GD, Group OG, *C. nemoralis*, Group G and Group GM. The intercept for other models represents predictions at the following conditions: visit 2 and railway–forest treatment for *C. erratus*, visit 1 and railway–forest treatment for *A. cursitans*, visit 2 and railway verge trap line for *A. municipalis*, and visit 2, railway–forest treatment and railway verge trap line for *P. niger* and *T. secalis*.

The intercept for Slovenian data also represents the prediction at visit 1, railway–forest treatment and railway verge trap line where possible, i.e. for *H. rufipes*, Group OD, *C. fuscipes*, *Amara* spp., *C. coriaceus*, *A. carinatus*, *C. granulatus* and Group GM. The intercept for *H. affinis*, *C. melanocephalus* and Group OG represents predictions at visit 1, railway–grassland treatment and railway verge trap line.

Note that treatment and trap line effects have been occasionally removed from a model if the species or species group did not occur in that particular treatment or trap line. Furthermore, interactions between treatment and matrix trap line were removed from models due to unsuitable outputs for Groups OG and GD in the Finnish data, and *H. rufipes*, *C. fuscipes* and Group GM in the Slovenian data.


a
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Built−up−railway
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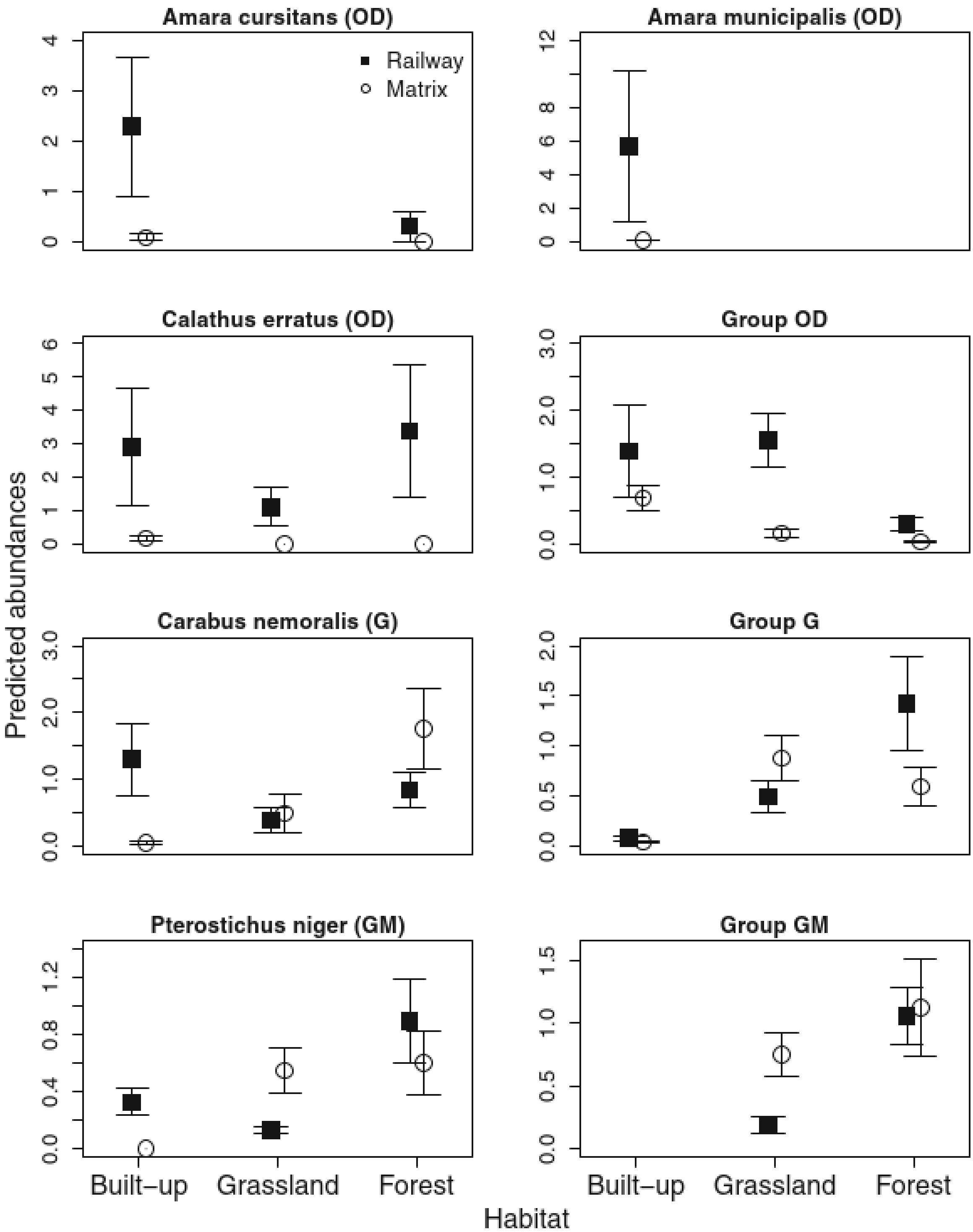
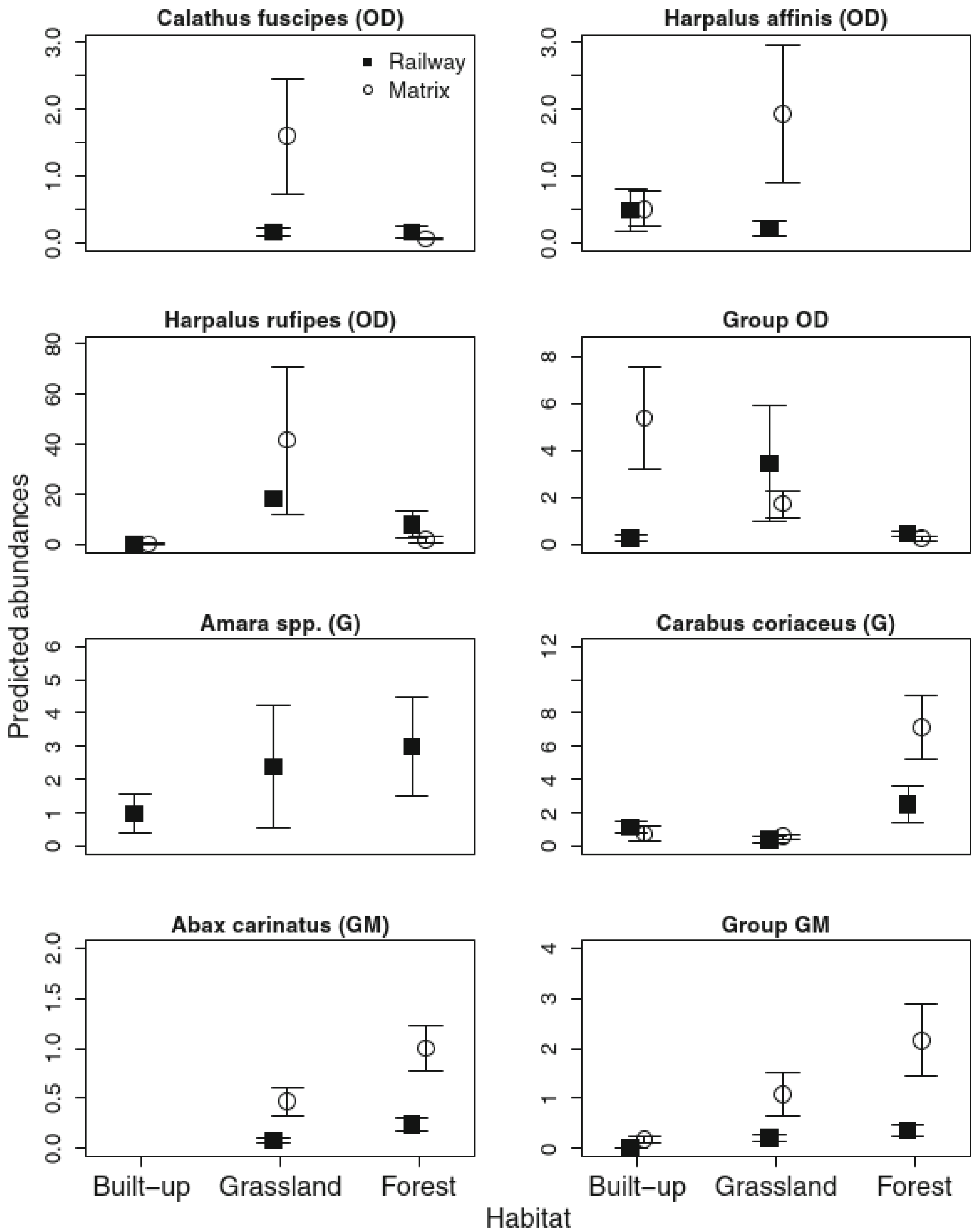


Amara cursitans (OD)
Railway
Matrix
Amara municipalis (OD)
Calathus erratus (OD)
Group OD
Carabus nemoralis (G)
Group G
Pterostichus niger (GM)
Group GM
Predicted abundances
Built−up
Grassland
Forest
Habitat

20


Calathus fuscipes (OD)
Railway
Matrix
Harpalus affinis (OD)
Harpalus rufipes (OD)
Group OD
Amara spp. (G)
Carabus coriaceus (G)
Abax carinatus (GM)
Group GM
Predicted abundances
Built–up
Grassland
Forest
Habitat

Online Resource 1 The number of individuals of all carabid beetle species collected from railway verges (R) and the adjacent matrices: built-up (B), grassland (G) and forest (F). Habitat associations are from Lindroth (1985, 1986) and Luff (2007) (Finnish species), and Müller (1930/31) and Müller-Motzfeld (2006) (Slovenian species). Abbreviations for habitat associations: OD = dry open habitat, OG = open habitat generalist, OM = moist open habitat, GD = dry habitat generalist, G = habitat generalist, GM = moist habitat generalist, FD = dry forest and FM = moist forest. Nomenclature for Finnish species follows Silfverberg (2004)

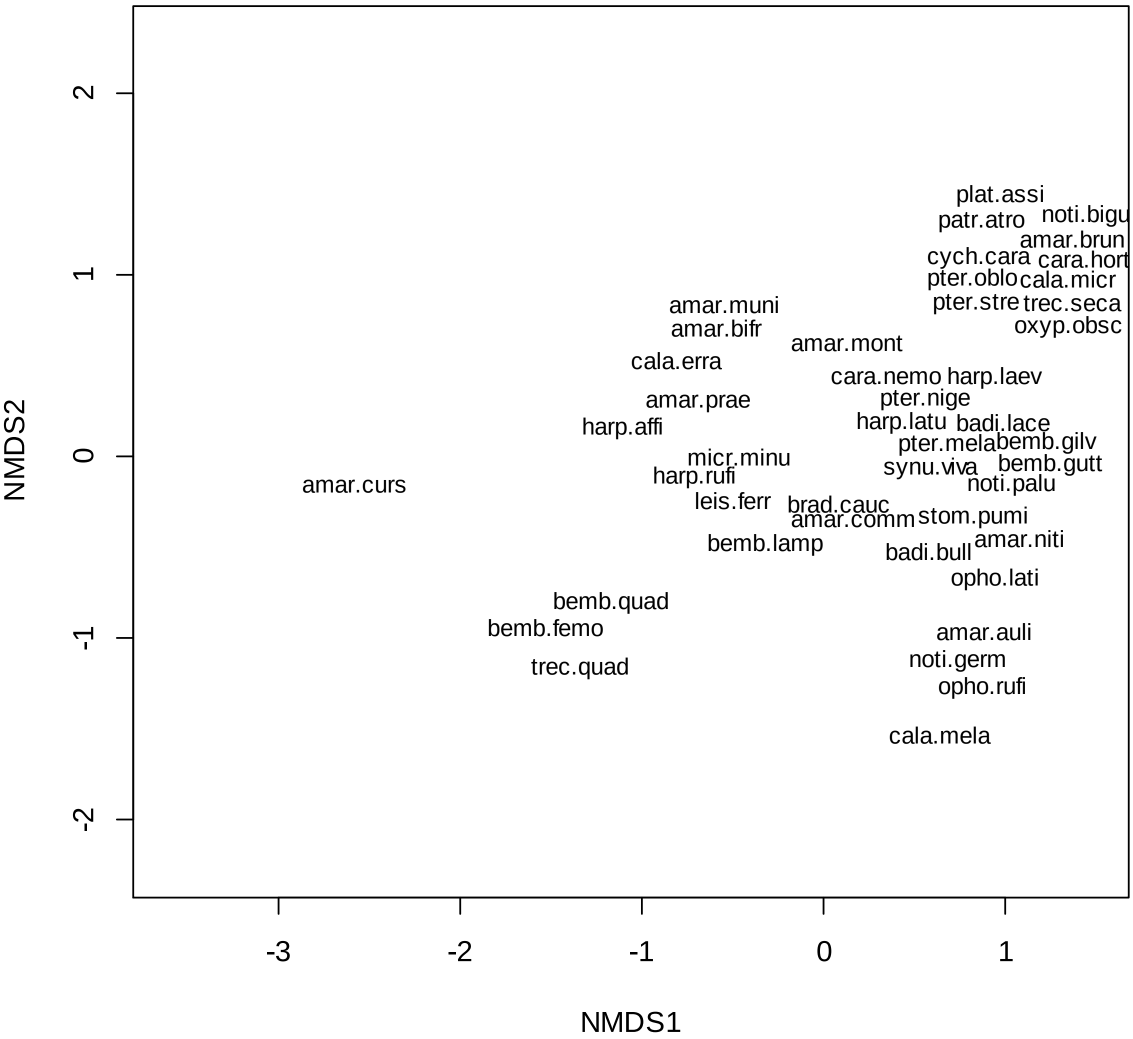
	GLMM [a]	Habitat	R	B	G	F	Total
Finland							
Amara aenea	Group OD	OD	0	1	0	0	1
Amara aulica	[b]	OM	0	0	5	0	5
Amara bifrons	Group OD	OD	23	2	0	0	25
Amara brunnea	[b]	FM	0	0	0	11	11
Amara communis	Group G	G	13	1	5	0	19
Amara convexior	Group OD	OD	1	0	0	0	1
Amara cursitans	species	OD	33	1	0	0	34
Amara familiaris	Group OG	OG	1	0	0	0	1
Amara montivaga	Group OD	OD	2	0	1	0	3
Amara municipalis	species	OD	69	1	0	0	70
Amara nigricornis	Group GD	GD	1	0	0	0	1
Amara nitida	Group OD	OD	6	0	0	0	6
Amara ovata	Group OD	OD	0	0	1	0	1
Amara praetermissa	Group OD	OD	11	0	0	0	11
Amara quenseli	Group OD	OD	1	0	0	0	1
Badister bullatus	Group G	G	5	0	3	1	9
Badister lacertosus	[b]	FM	5	0	3	2	10
Bembidion femoratum	Group OG	OG	5	27	0	0	32
Bembidion gilvipes	Group GM	GM	0	0	5	0	5
Bembidion guttula	Group GM	GM	0	0	6	1	7
Bembidion lampros	Group OD	OD	5	2	0	0	7
Bembidion quadrimaculatum	Group OG	OG	2	7	0	0	9
Blemus discus	[b]	OM	0	0	1	0	1
Bradycellus caucasicus	Group OD	OD	4	0	0	0	4
Calathus erratus	species	OD	122	1	0	0	123
Calathus melanocephalus	Group OD	OD	1	0	2	0	3
Calathus micropterus	[b]	FD	2	0	0	36	38
Carabus hortensis	[b]	FD	0	0	0	13	13
Carabus nemoralis	Group OG	OG	51	1	10	35	97
Cychrus caraboides	[b]	FM	2	0	0	12	14
Cymindis angularis	Group OD	OD	1	0	0	0	1
Dicheirotrichus placidus	Group GM	GM	0	0	1	0	1
Dyschirius globosus	[b]	OM	1	0	0	0	1
Harpalus affinis	Group OD	OD	4	1	0	0	5
Harpalus laevipes	Group GM	GM	10	0	0	0	10
Harpalus latus	Group G	G	11	0	4	0	15
Harpalus rufipes	Group OG	OG	7	4	2	0	13
Harpalus tardus	Group OD	OD	0	1	0	0	1
Leistus ferrugineus	Group OD	OD	1	1	0	1	3
Microlestes minutulus	Group OD	OD	3	1	0	0	4

Notiophilus aquaticus	Group OD	OD	2	0	0	0	2
Notiophilus biguttatus	[b]	FD	0	0	0	7	7
Notiophilus germinyi	Group OD	OD	3	0	0	0	3
Notiophilus palustris	Group GM	GM	4	0	1	1	6
Ophonus laticollis	Group GD	GD	26	0	0	0	26
Ophonus rufibarbis	[b]	OM	45	0	57	0	102
Oxypselaphus obscurus	[b]	FM	3	0	0	7	10
Patrobus atrorufus	Group GM	GM	1	0	0	3	4
Platynus assimilis	[b]	FM	0	0	0	3	3
Poecilus versicolor	Group OG	OG	1	0	1	0	2
Pterostichus melanarius	Group G	G	8	0	6	10	24
Pterostichus niger	species	GM	28	0	11	12	51
Pterostichus oblongopunctatus	[b]	FD	3	0	0	14	17
Pterostichus strenuous	Group GM	GM	5	0	0	13	18
Stomis pumicatus	Group G	G	6	0	1	2	9
Synuchus vivalis	Group GD	GD	6	0	4	0	10
Trechoblemus micros	[b]	OM	2	0	0	0	2
Trechus quadristriatus	Group OD	OD	0	6	0	0	6
Trechus secalis	species	GM	35	0	20	92	147
Total number of individuals for Finland			581	58	150	276	1065
Total number of species for Finland			46	16	22	20	59
Slovenia							
Abax carinatus	species	GM	8	0	11	22	41
Abax parallelepipedus	Group GM	GM	6	0	0	3	9
Abax parallelus	[b]	GM	1	0	0	146	147
Agonum sp.	Group GM	GM	0	0	0	13	13
Amara spp.	Species	G	102	4	6	0	112
Anchomenus dorsalis	Group OD	OD	4	0	10	0	14
Anisodactylus nemorivagus	Group GM	GM	0	0	2	0	2
Anisodactylus signatus	Group GM	GM	3	2	5	0	10
Apristus europaeus	Group GD	GD	1	0	0	0	1
Asaphidion flavipes	Group G	G	0	0	0	2	2
Bembidion properans	Group OM	OM	0	0	1	0	1
Brachinus elegans	[b]	OD	31	0	92	0	123
Brachinus explodens	Group OD	OD	2	0	0	0	2
Bradycellus caucasicus	Group GD	GD	2	0	0	1	3
Calathus fuscipes	species	OD	8	0	36	0	44
Calathus melanocephalus	species	OD	2	0	38	0	40
Calistus lunatus	Group OD	OD	4	0	0	0	4
Carabus catenulatus	[b]	FG	0	0	0	10	10
Carabus coriaceus	species	G	85	14	14	144	257
Carabus germari	[b]	FG	3	0	2	3	8
Carabus granulatus	species	GM	6	0	9	45	60
Carabus variolosus	[b]	FM	0	0	0	1	1
Chlaenius nitidulus	Group OM	OM	1	0	3	0	4
Clyndera germanica	[b]	OD	7	1	140	0	148
Cychrus attenuates	[b]	FM	0	3	0	35	38

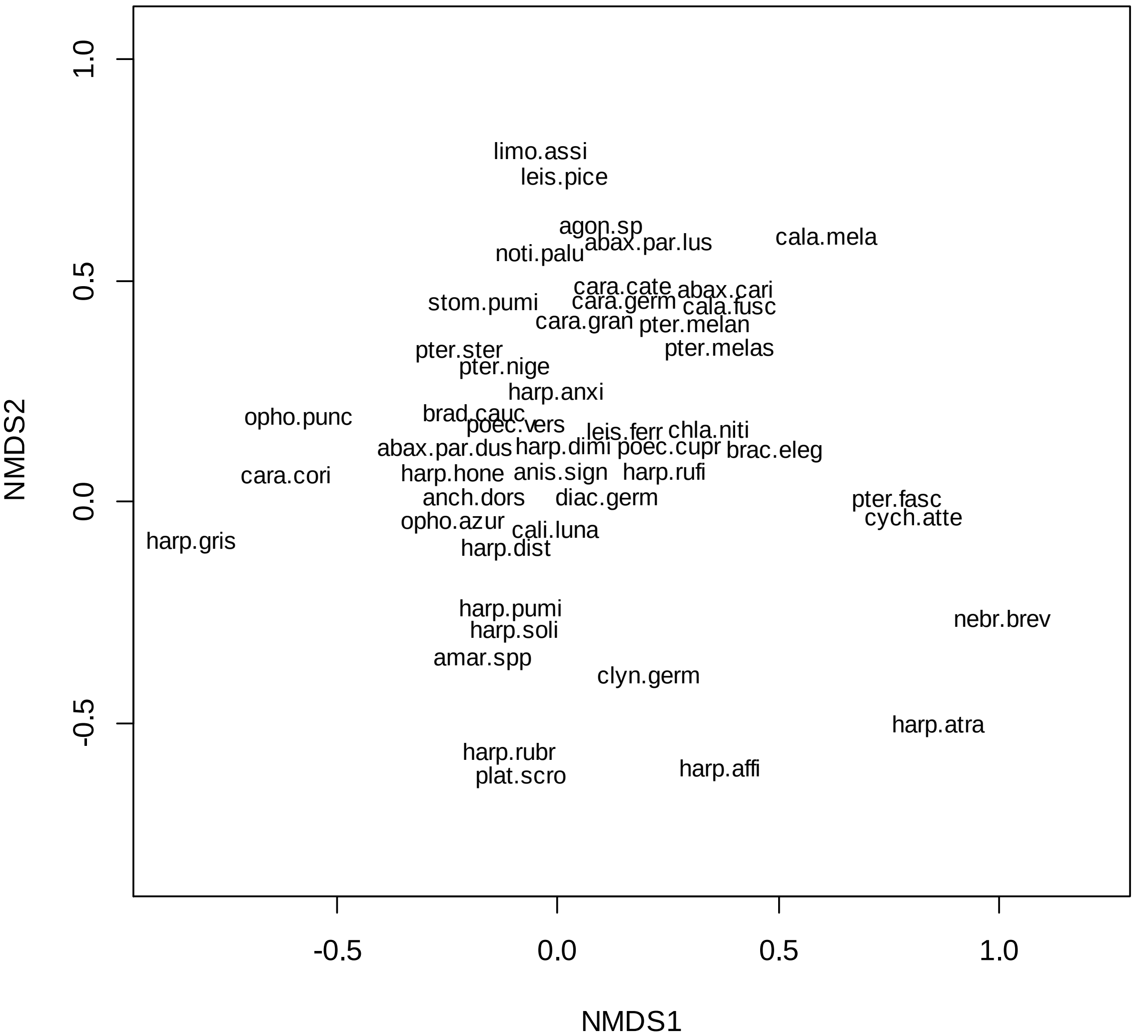
Cychrus caraboides	[b]	FM	1	0	0	0	1
Diachromus germanus	[b]	OD	23	0	16	0	39
Dolichus halensis	Group OG	OG	0	0	1	0	1
Elaphrus aureus	Group GM	GM	0	0	0	1	1
Harpalus affinis	species	OD	12	8	32	0	52
Harpalus anxius	Group OD	OD	2	0	5	0	7
Harpalus atratus	Group OD	OD	2	19	1	2	24
Harpalus dimidiatus	Group OG	OG	15	0	14	0	29
Harpalus distinguendus	[b]	OD	62	3	31	0	96
Harpalus griseus	Group OD	OD	2	1	0	0	3
Harpalus honestus	[b]	OD	117	0	0	0	117
Harpalus karamani	Group OD	OD	0	0	1	0	1
Harpalus luteicarnis	Group GD	GD	0	0	1	0	1
Harpalus pumilus	[b]	OD	52	0	0	0	52
Harpalus punctipennis	Group OD	OD	0	1	0	0	1
Harpalus rubripes	Group OD	OD	8	9	1	0	18
Harpalus rufipes	species	OD	516	8	836	43	1403
Harpalus solitaris	Group OD	OD	7	0	0	0	7
Harpalus sp.	Group OD	OD	0	0	1	1	2
Harpalus subcylindricus	Group OD	OD	0	0	1	0	1
Harpalus tenebrosus	Group GD	GD	0	2	0	0	2
Leistus ferrugineus	Group GM	GM	2	0	4	0	6
Leistus piceus	Group GM	GM	0	0	1	9	10
Limodromus assimilis	[b]	FM	0	0	0	7	7
Microlestes minutulus	Group OD	OD	1	0	0	0	1
Molops striolatus	[b]	FG	0	0	0	1	1
Nebria brevicollis	Group GM	GM	0	1	5	0	6
Notiophilus palustris	Group GM	GM	1	0	0	2	3
Notiophilus rufipes	Group GD	GD	0	0	2	0	2
Ophonus azureus	Group OD	OD	7	23	2	0	32
Ophonus puncticollis	Group OD	OD	13	7	1	1	22
Platynus scrobiculatus	Group GM	GM	0	1	0	2	3
Poecilus cupreus	[b]	OM	83	0	530	0	613
Poecilus versicolor	Group OG	OG	2	0	13	0	15
Pterostichus fasciatopunctatus	[b]	FM	0	2	0	30	32
Pterostichus melanarius	Group GM	GM	1	0	3	3	7
Pterostichus melas	[b]	G	4	0	121	2	127
Pterostichus niger	Group GM	GM	1	0	2	5	8
Pterostichus nigrita	Group GM	GM	0	0	0	1	1
Pterostichus rhaeticus	Group GM	GM	1	0	0	1	2
Pterostichus sternuus	Group GM	GM	0	1	0	2	3
Stomis pumicatus	Group GM	GM	0	0	1	3	4
Synuchus vivalis	Group OG	OG	0	0	1	1	2
Trechus croaticus	[b]	FG	0	0	0	1	1
Trechus quadristriatus	Group G	G	1	0	0	0	1
Total number of individuals for Slovenia			1212	110	1996	543	3861
Total number of species for Slovenia			43	19	40	32	70

[a] The GLMM column shows if a species was analysed individually in the generalised linear mixed models or if it was pooled into groups based on habitat association.

[b] Species were removed from GLMM analyses based on three criteria: 1) a species was abundant but the data were highly clumped, 2) forest species were not analysed, as they occurred almost exclusively in forests, and 3) Group OM was excluded due to low numbers of individuals.



Online Resource 2 Non-metric multidimensional scaling ordination (NMDS) of Finnish carabid beetle species at the railway–matrix treatments (i.e. railway–built-up, railway–grassland and railway–forest). See Fig. 1 in the manuscript for the NMDS site plot. Species name abbreviations consist of the first four letters of the genus name and first four letters of the species name (for full species names, see Online Resource 1)



Online Resource 3 Non-metric multidimensional scaling ordination (NMDS) of Slovenian carabid beetle species at the railway–matrix treatments (i.e. railway–built-up, railway–grassland and railway–forest). See Fig. 1 in the manuscript for the NMDS site plot. Species name abbreviations consist of the first four letters of the genus name and first four letters of the species name (for full species names, see Online Resource 1)

Online Resource 4 Correlations (r^2) and p-values of the environmental variables used in the non-metric multi-dimensional scaling ordinations for the Finnish and Slovenian carabid beetle datasets. The vegan function envfit (see Oksanen et al. 2013) was used to test the fit of these variables using permutation tests

Environmental variable	Finland		Slovenia	
	r^2	p-value	r^2	p-value
Soil moisture (%)	0.471	**0.003**	0.356	**0.010**
Urbanisation degree [a]	0.375	**0.007**	0.339	**0.013**
Rock cover (%)	0.376	**0.012**	0.319	**0.017**
Bare soil cover (%)	0.511	**0.001**	0.273	**0.035**
Litter cover (%)	0.418	**0.005**	0.278	**0.032**
Soil pH	0.466	**0.002**	0.198	**0.099**
Shrub cover (%)	0.197	0.122	0.116	0.276
Ground-layer vegetation cover (%) [b]	0.421	**0.004**	0.061	0.516
Distance (m) [c]	0.158	0.178	0.076	0.436
Verge width (m)	0.037	0.691	0.060	0.523
Slope (°)	0.007	0.932	0.038	0.670

Significant p-values are in boldface. [a] Urbanisation degree represents % imperviousness or urbanised land within a 500 m buffer for Finland and Slovenia respectively. [b] Ground-layer vegetation cover includes grass, herb and moss. [c] Distance between railway and matrix trap lines.

Online Resource 5 Environmental variables (means ± SD) within railway verges and the adjacent matrices at the railway–built-up, railway–grassland and railway–forest treatments

Environmental variables		Built-up Railway	Built-up Matrix	Grassland Railway	Grassland Matrix	Forest Railway	Forest Matrix
Finland							
Ground-layer vegetation cover (%) [a]	mean	24.5	10.0	46.0	94.3	25.0	21.5
	(SD)	(19.7)	(5.3)	(42.4)	(9.5)	(18.3)	(6.9)
Shrub cover (%)	mean	4.0	0.0	3.0	0.8	17.3	18.5
	(SD)	(4.7)	(0.0)	(3.2)	(1.0)	(28.0)	(23.4)
Litter cover (%)	mean	13.3	3.3	14.8	10.3	19.0	75.8
	(SD)	(11.2)	(3.5)	(15.1)	(6.7)	(10.2)	(9.7)
Rock cover (%)	mean	5.8	19.0	18.8	0.0	19.5	0.0
	(SD)	(8.9)	(32.9)	(26.6)	(0.0)	(19.0)	(0.0)
Bare soil cover (%)	mean	56.8	70.0	23.3	1.5	21.0	0.0
	(SD)	(37.5)	(39.9)	(43.9)	(3.0)	(14.0)	(0.0)
Verge width (m)	mean	4.5		4.3		3.7	
	(SD)	(2.2)		(2.8)		(2.4)	
Distance (m) [b]	mean	16.8		14.6		20.5	
	(SD)	(2.4)		(7.1)		(5.2)	
Slope (°)	mean	7.5	0.0	25	2.5	17.5	3.8
	(SD)	(6.5)	(0.0)	(7.1)	(2.9)	(13.2)	(4.8)
Urbanisation degree [c]	mean	42.3	42.3	33.5	33.5	25.5	25.5
	(SD)	(4.6)	(4.6)	(9.3)	(9.3)	(2.6)	(2.6)
Soil pH	mean	6.9	7.0	6.4	6.1	5.8	5.3
	(SD)	(0.4)	(0.8)	(0.4)	(0.1)	(0.3)	(0.8)
Soil moisture content (%)	mean	0.9	1.1	5.9	13.8	1.8	28.7
	(SD)	(0.9)	(1.2)	(5.9)	(3.0)	(1.9)	(16.7)
Soil organic matter content (%)	mean	2.2	2.7	3.4	11.2	1.2	48.6
	(SD)	(1.2)	(2.2)	(3.1)	(2.4)	(0.3)	(29.9)
Slovenia							
Ground-layer	mean	15.0	34.3	7.3	81.8	29.8	10.5

vegetation cover (%) [a]	(SD)	(11.2)	(33.5)	(6.4)	(7.8)	(16.3)	(3.7)
Shrub cover (%)	mean	3.5	19.8	3.8	7.3	2.8	10.5
	(SD)	(3.0)	(19.4)	(5.7)	(6.4)	(3.6)	(11.4)
Litter cover (%)	mean	3.5	9.8	6.3	6.5	13.8	82.0
	(SD)	(3.1)	(9.5)	(8.1)	(1.3)	(8.5)	(5.0)
Rock cover (%)	mean	76.8	12.8	63.0	0.0	48.3	0.0
	(SD)	(13.2)	(17.6)	(33.4)	(0.0)	(27.3)	(0.0)
Bare soil cover (%)	mean	1.5	24.0	18.8	7.0	8.0	0.8
	(SD)	(2.4)	(14.1)	(22.3)	(8.1)	(13.5)	(1.0)
Verge width (m)	mean	3.1		0.8		2.0	
	(SD)	(1.7)		(0.6)		(0.5)	
Distance (m) [b]	mean	126.9		43.8		27.8	
	(SD)	(99.3)		(14.7)		(10.9)	
Slope (°)	mean	9.5	5.5	20.0	1.0	14.0	5.5
	(SD)	(12.8)	(9.1)	(13.9)	(2.0)	(11.7)	4.9
Urbanisation degree [c]	mean	98.2	98.1	60.2	54.5	14.3	14.3
	(SD)	(2.2)	(1.9)	(35.4)	(28.7)	(6.7)	(7.0)
Soil pH	mean	8.5	8.4	8.4	7.3	8.2	6.5
	(SD)	(0.4)	(0.3)	(0.8)	(0.5)	(0.8)	(2.3)
Soil moisture (%)	mean	6.1	6.5	8.4	18.7	12.2	27.7
	(SD)	(5.5)	(3.7)	(8.5)	(1.5)	(10.4)	(14.0)
Soil organic matter (%)	mean	7.7	8.1	7.1	11.4	14.2	25.4
	(SD)	(3.4)	(2.7)	(5.1)	(2.5)	(9.0)	(22.3)

[a] Ground-layer vegetation cover includes grass, herb and moss. [b] Distance between railway and matrix trap lines. [c] Urbanisation degree represents % imperviousness or urbanised land within a 500 m buffer for Finland and Slovenia respectively.