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Research Article

Highways and forest fragmentation – effects on carabid beetles (Coleoptera, Carabidae)

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Abstract

We conducted two studies on how highways affect their adjacent habitats by sampling carabid beetles (Coleoptera, Carabidae) in patches of formerly continuous forest next to highways. (1) We sampled carabids at 14 highway intersections near Helsinki, Finland. Each intersection (constructed 2–40 years ago) had two forested patches to study: a remnant (0.5–37.4 ha) and, isolated from the remnant by an intersection lane, an islet (size 0.2–1.8 ha). Pitfall trap catch data (2301 carabids, 25 species) showed that remnants hosted higher catches of three carabid species, and slightly higher species richness, than islets (patch-size effect). Time since intersection construction had no apparent effect on carabids. Traffic volume along the intersection lane determined the assemblage structure of carabids in dry patches, and the abundance of a forest carabid *Calathus micropterus*. Compared to moist patches, drier patches hosted lower catches of four generalist species; they also had different assemblages of carabids (habitat-type effect). An interaction between patch size and habitat type for a forest generalist *Pterostichus oblongopunctatus* indicated that the patch-size effect was dependent on habitat type. (2) We examined possible dispersal of carabids among forested patches that were separated by highway lanes in Drenthe, the Netherlands. We released 2696 marked individuals of 10 species, and recaptured 376 using dry pitfall traps. We found no evidence for inter-patch movement for nine forest species, but 22 of 225 recaptured individuals of *Poecilus versicolor*, an eurytopic open-habitat species, had crossed the highway. Catches of seven forest species were also significantly lower in the road verges, compared to the adjacent forests. These two studies suggest that (i) decreasing patch size negatively affects forest-carabid catch and overall species richness, (ii) habitat type can affect the intensity of the patch-size effect, (iii) carabid assemblages of forest fragments vary with traffic volume (which may be linked with urbanization), (iv) forest carabids rarely cross highways, and (v) open habitats associated with road margins are dispersal barriers for forest carabids.

Introduction

Roads and their construction affect the biota directly and indirectly (Forman and Alexander 1998; Hourdequin 2000; Trombulak and Frissell 2000). Direct effects of road construction include alteration of original habitat, deaths of individuals, and changes in soil chemical properties, water balance and microclimate of habitats (Forman et al. 2003). Moreover, collisions with cars cause additional animal injuries and deaths that may threaten populations (Gloyne and Clevenger 2001; Dickson and Beier 2002). Roadways modify animal behavior (Dyer et al. 2002), and may enhance the dispersal of exotic species (e.g. Niemelä and Spence 1999). Not all known effects are negative, as some species, even endangered ones, may benefit from grassy verges of roadsides (e.g. Eversham and Telfer 1994; Vermeulen 1994; Eisto et al. 2000). Moreover, even completely asphalt-isolated, narrow grassy strips may host rich beetle assemblages that include endangered species (Koivula and Kotze 2005).

Perhaps most significantly for subsequent development of biotic communities, roads also fragment habitat, and thereby affect dispersal and spatial distribution of organisms. Small habitat patches, physically isolated by roads, include only samples of the original larger population or assemblage, and individual movements between patches may be hampered (Mader et al. 1990). For example, Mader (1984) showed that carabid beetles (Coleoptera, Carabidae) are reluctant to cross paved roads, but are guided to move along them. Moreover, Koivula (2003) showed that even narrow (width 3–5 m) unpaved forest roads favor open-habitat and habitat-generalist carabids, whereas a forest species showed the opposite response.

We studied carabid assemblages in forest patches isolated from earlier continuous forest by highway construction, and report results from studies in Finland and in the Netherlands that contribute to understanding the effects of roads on carabids. We examined three issues: (1) how road construction affects habitat quality in isolated patches, (2) whether highway traffic volume affects carabid populations in fragments adjacent to these roads, and (3) whether carabids cross wide, paved highway lanes.

More specifically, we stated the following hypotheses.

(1) Highway intersections often have a completely isolated patch of trees (here referred to as an islet) and adjacent larger remnant forest (here referred to as a remnant), from where the islet has been isolated by the intersection construction, as in the sites of the Finnish study. The islets are expected to host fewer individuals of carabids associated with forested habitats, whereas carabids of open habitats and forest/open-habitat generalists should show an opposite response, as earlier shown by Halme and Niemelä (1993) for isolated, small forest patches.

(2) Traffic volume along the lanes that separate islets and remnants should affect the mortality of possible highway crossers, and thereby contribute to the isolation of islets.

(3) The similarity between assemblages in the islet and the remnant should decrease with the duration of the isolation, assuming that the islets are truly isolated from remnants.

(4) Habitat quality (soil moisture, shadiness) should affect carabid catches (Thiele 1997), as earlier shown for Finnish spruce forests by Koivula (2002).

(5) Highway lane crossings by carabids are expected to be rare, as earlier shown by Mader et al. (1990). Species associated with open habitat might cross the lanes more frequently than forest-habitat specialists because of the general avoidance of open areas by the latter.

(6) The fine-scale abundance variation of carabids may contribute to the possible barrier effect of a highway on forest carabids (see reasoning in hypothesis 5). Forest specialists are expected to be less frequently trapped at the highway verges, compared to the adjacent forests.

Material and methods

Carabids in forested patches along highways

We sampled carabids at 14 highway intersections that were constructed 2–40 years ago (data from the Finnish Road Administration) in southern Finland between 28 May and 10 September 2002 (Figure 1). Each intersection included an islet [0.2–1.8 ha, average 0.79 ± 0.12 (SE) ha] completely isolated by highway and an adjacent remnant [0.5–37.4 ha, average 10.38 ± 3.02 (SE) ha] of the original forest. At any given intersection the remnant was a minimum of 40% larger than the islet, except for two intersections with ca. 20% difference. Conifers [Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*)] dominated the forests at all patches, with aspen (*Populus tremula*) and birches (*Betula pubescens* and *B. pendula*) as more minor components. Predominant canopy trees were

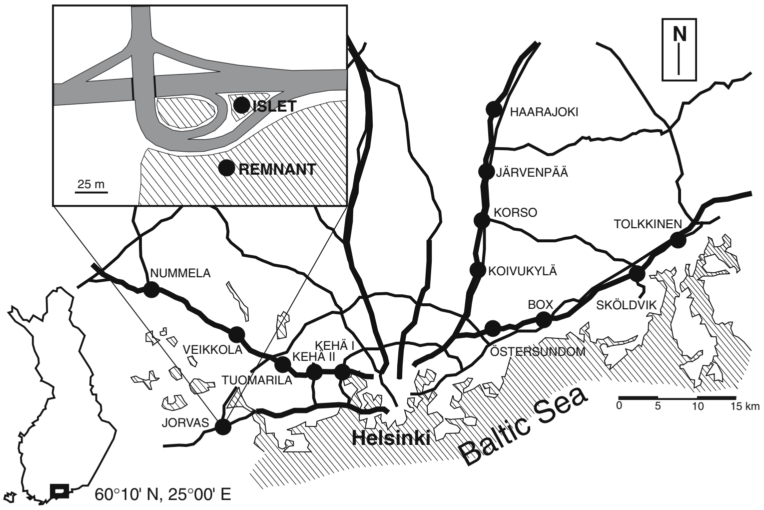

Figure 1. Sampling design in Finland in 2002. The larger figure shows the 14 study intersections and main highways (motorways with thicker line), and the cross-hatched areas represent water. The vignette (left) shows an example intersection (Jorvas, Highway nr. 51) with terminology used in this paper, along with the spatial arrangement of the groups of four pitfall traps (black circles); land area covered by forest is cross-hatched, highway is grey; REMNANT = the remnant-forest patch, ISLET = the islet patch.

60–120 years old. The field layer usually consisted of *Vaccinium myrtillus* dwarf shrubs, and *Pleurozium* and *Dicranum* mosses. Some trapping sites had more lush vegetation, with more birches than spruce, and with the field layer partially covered with more mesic plants such as *Convallaria majalis* and *Anemone nemorosa*, and various grasses (e.g. *Calamagrostis* spp.).

We included one sampling site each in the islet and in the remnant at each intersection. Each sampling site had four plastic pitfall traps (mouth diameter 88 mm, depth 90 mm, 30% propylene glycol with detergent, 10 cm × 10 cm styrene roof to protect the trap from litter and rain) arranged into 4 m × 4 m squares. Because the smallest islet was only 0.2 ha, we placed all the traps consistently 10–20 m from the forest-patch edge to rule out possible biases on the catches. Within each intersection, we placed the islet and remnant trap groups as close to each other as possible. Only occasional samples were lost; sampling periods were pooled (because of many low period-specific catches), the data were adjusted to $n/50$ days × patch, and log $(n + 1)$ transformed to approach normality before analyses.

Traffic volume along the studied highways varied from 17,000 to over 40,000 vehicles/24 h in the summer of 2002. However, along the intersection lane that divided the remnants from the islets, the traffic volume was remarkably lower, varying from 860 to 14,000 vehicles/24 h (data from the Finnish Road Administration). As expected, the highway and intersection-lane volume values were highly correlated with each other (Spearman rank correlation; $r_s = 0.75$, $p = 0.003$).

For the Finnish data, we analyzed (i) the total carabid catch, (ii) carabid species richness, and (iii) abundance of carabid species with $n > 50$ and found in > 10 intersections using General Linear Models (GLM; Jongman et al. 1995; Legendre and Legendre 1998). We tested the effects of 'Patch type' (islet vs. remnant), 'Traffic' (volume along the lane between the islet and remnant), 'Time' (time since intersection construction), and 'Habitat' (habitat variation; patches classified into dry, medium-moist and moist, based on tree-species and dominant field-layer vegetation composition). We included habitat type in the model as it may contribute to the results; the islets are potentially of drier types. Islets included 4 dry, 5 medium-moist and 5 moist trapping sites, and remnants included 3, 7 and 4 sites, respectively. The continuous variables Traffic and Time were uncorrelated with each other ($r_s = -0.16$, $p = 0.584$).

We also included three interaction terms to examine possible carabid response differences between remnants and islets: Patch type × Traffic, Patch type × Time, and Patch type × Habitat. An interaction between patch type (islet vs. remnant; ~patch size) and traffic volume should be detected, if the increasing traffic volume decreases carabid lane crossings and thereby contributes negatively to the carabid abundances, especially in the islets. Furthermore, if the islets are truly isolated from remnants, an interaction between patch type and isolation time should be detected, because dispersal among habitat patches is considered important for the persistence of local populations (e.g. De Vries 1996; Hanski 1999). Even if small populations of forest carabids *could* persist in the small patches for some time, they may go extinct due to the environmental stochasticity (e.g. Tilman et al. 1994; Loehle and Li 1996). Habitat type might affect the patch-type effect. Thus, habitat quality (e.g. soil moisture and vegetation) may determine how severely carabids are affected by edge effects; carabids might thus respond to patch size habitat type specifically.

We further studied the assemblage-level responses on the above-listed four GLM variables by subjecting non-transformed data to Non-metric Multidimensional Scaling (NMDS; Borg and Groenen 1997), and Multivariate Regression Trees (MRT; De'ath 2002). In NMDS and MRT, we used Bray-Curtis pair-wise similarities between samples, and included all the species. We ran NMDS until we got the lowest stress value twice, and selected the resultant sample (patch) and species scores as the best model. We then plotted the patch scores along first two dimensions, and examined the importance of GLM variables visually by classifying the scores accordingly. MRT, on the other hand, identifies groups of sites defined by environmental (here, GLM) variables and can potentially account for nonlinearity (De'ath 2002). The result is usually presented as a tree of dichotomies. Each dichotomy is chosen to minimize the dissimilarity of sites within each branch. We did the final tree selection by detecting the tree size (number of 'end' branches) that had the lowest cross-validated relative error, following the 1-SE rule by Breiman et al. (1998; see also De'ath 2002). We combined MRT with Indicator Value calculations (IndVal; Dufrêne and Legendre 1997) for the abundant species ($n > 10$) falling into the MRT branches. The IndVal calculus contrasts the presence/absence and abundance among sites of a given MRT branch with those among the rest of the sites. For each branch, each included species gets a value that varies from 0 (not present in a given group of sites) to 100 (perfect indicator; present in all samples within a given group of sites but completely absent from all the other sites). After a species has reached its maximum IndVal, it is not presented in the subsequent branches any further. We also combined MRT and IndVal with plots of all the species for each MRT branch. Here, the species-specific mean catches for each tree branch were plotted, using the rank-abundance order determined by the overall catch.

We carried out the analyses using R 2.0.1 (R Development Core Team 2004), except for the IndVal calculations that were performed using IndVal 2.0 (Dufrêne 1998).

Mark-recapture of carabids adjacent to highway lanes

We studied lane crossings by carabids in the Netherlands in 1993–1994, adjacent to a two-lane highway constructed in 1958 through the ca. 50 ha Nuiler forest in Drenthe. The highway divided the forest into two parts (western ca. 19 ha and eastern ca. 14 ha). The western part was further divided into a larger remnant and a 0.5-ha central reservation strip in 1972, when the original two-lane road was widened into a four-lane highway. In the study years, the traffic along the highway was approx. 35,000 vehicles/24 h. The forest canopy was dominated by European white birch (*Betula pendula*) and Pedunculate oak (*Quercus robur*), with *Betula pubescens*, *Quercus petraea* and *Pinus sylvestris* as more minor elements. *Vaccinium myrtillus* dominated the field-layer vegetation in the forest, but the road verges were mostly covered by grass that became denser closer to the pavement (authors' pers. obs.).

We used dry pitfall traps (diameter 100 mm) to collect and re-capture marked carabids on both sides and in the central reservation strip of the highway. We placed nine 10-trap transects, with an inter-trap distance of 2 m, parallel to the roadways (Figure 2). Adjacent transects were separated by 14 m. We serviced the traps twice a week, from early April to mid-November.

We marked individuals of 10 carabid species in 1993, following methods of Schøtz-Christensen (1965). Five species were forest dwellers with poor or no flight ability, four species were generalist forest-habitat species with known good dispersal

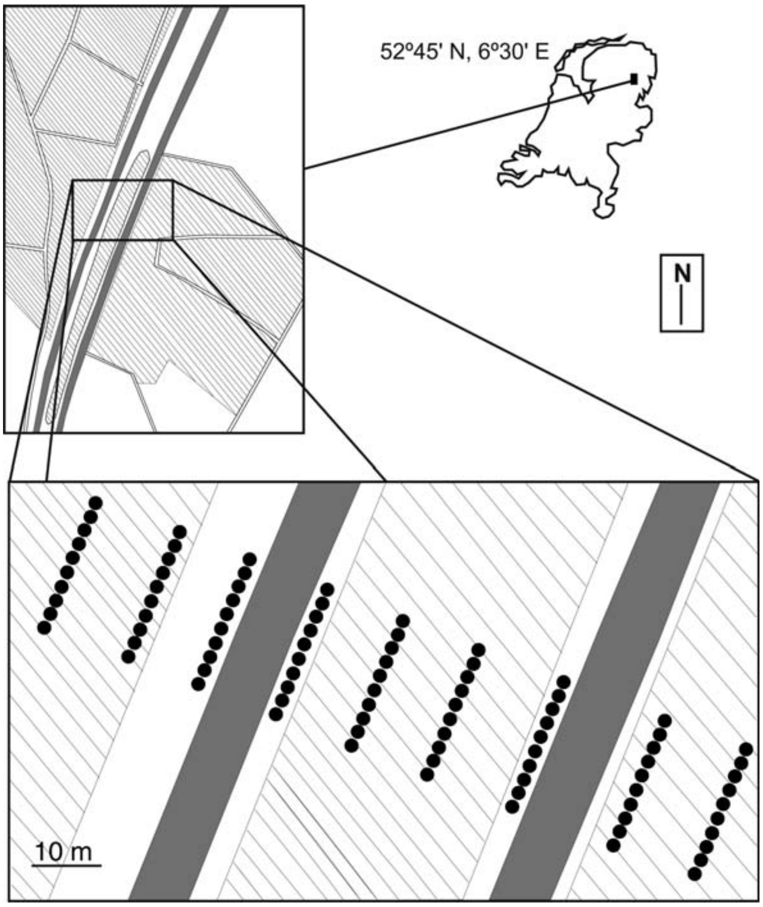

Figure 2. Sampling design at the roadsides of the Nuiler forest, the Netherlands, in 1993–1994. Black dots indicate pitfall traps; white is grassy road verge, cross-hatched areas are forest, and highway is grey.

ability, and one species – *Poecilus versicolor* – represented carabids of grassy, open habitats. Recaptured beetles were released within a few meters from the trap row where they were captured, during the day of capture.

We used catches of pooled periods in the analyses, keeping transects separate. As the numbers of recaptures differed remarkably between those that did cross the highway and those that did not, we did not analyze this result statistically; for example, if the compared *n*'s are 6 (or much higher as in our data) and 0, with expected value 3, the χ^2 probability is always <0.05. However, to study the habitat-use specificity of carabids, we compared the species-specific catches of forest transects to those of the verges using G^2 test with Williams' adjustment (Sokal and Rohlf 1995). Because we had more transects in the forests than in the verges (6 vs. 3), we randomly selected three out of the six forest transects to represent forest samples in the analysis. The null hypothesis was that there was no difference between forest and verge samples; thus, the expected value was (species specifically) the average of forest and verge catch.

Results

Carabids in forested patches along highways

The Finnish dataset consisted of 2301 carabid individuals, representing 25 species (Appendix 1). Of these, 17 species were represented by at least four individuals, and all of these were caught in at least one islet. The most abundant species were *Pterostichus niger* (45.0% of the total catch), *Pterostichus melanarius* (16.7%), *Carabus hortensis*

Table 1. Summary of GLM results for the Finnish intersection dataset.

Group/species	Patch	Traffic	Time	Habitat[a]	Interactions
Total catch	ns	ns	ns	+	none
Species richness	(+)	ns	ns	ns	none
Calathus micropterus (Dft.)	+	(–)	ns	ns	none
Carabus hortensis L.	(+)	ns	ns	ns	none
Carabus nemoralis Müll.	ns	ns	ns	(+)	none
Cychrus caraboides (L.)	ns	ns	ns	ns	none
Pterostichus melanarius Ill.	ns	ns	ns	+ +	none
P. niger (Sch.)	ns	ns	ns	+ +	none
P. oblongopunctatus (F.)	+ +	ns	ns	+ +	Patch × Habitat

For analysis details, consult Appendix 2. Patch = patch-type effect (~patch size) tested; Traffic = traffic volume tested; Time = time since intersection construction tested; Habitat = habitat-type effect tested; Interactions = significant interactions ($p < 0.05$) among the four main factors listed. One symbol (+ for positive, – for negative effect) = $p < 0.05$; two symbols (+ +) = $p < 0.01$; symbol in parentheses = $p < 0.1$; ns = $p \geq 0.1$.

[a] Habitats were classified into dry, moderately moist and moist, based on tree-species composition and field-layer dominant vegetation. Significances for Habitat column are after *post hoc* test; '+' indicates that the moist patches had higher catches than the drier ones.

(10.3%) and *Carabus nemoralis* (8.4%). Catches of the 17 most abundant species were generally lower in the islets than in the remnants (Appendix 1). Many individuals of three forest-associated carabids were caught even in the smallest patches: *C. hortensis*, *Cychrus caraboides*, and *Calathus micropterus*. For example, total catch of these species for the 11 patches < 1 ha were 78, 19 and 30 individuals, respectively, and for all the 17 patches < 1.5 ha, the respective totals were 127, 26 and 57.

The GLM variables altogether explained from 27.5% (*C. caraboides*) to 70.5% (*P. oblongopunctatus*) of the variation in the data (Table 1; for analysis details, consult Appendix 2). If significant differences were detected (see below), they consistently indicated that (a) the remnants hosted higher catches than the islets, and (b) moist patches hosted higher catches than drier ones (Appendix 2). Also, an effect of traffic volume was found (see below).

The total carabid catch was significantly affected by habitat moisture class, and this variable explained 27.8% of the variation; as expected, the moist patches hosted more individuals than the two drier habitat classes (Table 1). Species richness was slightly higher in the remnants, compared to the islets; patch type explained 14.0% of that variation. No other model variables or their interactions were significant.

The seven species abundant enough for population comparisons were all on average captured more commonly in the remnants than in the islets (Figure 3). However, only *C. micropterus* and *P. oblongopunctatus*, and marginally *C. hortensis*, were significantly more abundant in remnants (Table 1). For these three species, patch type explained 20.4, 24.4 and 13.9% of the respective variation in catch. Catches of the three *Pterostichus* species were clearly higher in the moist-habitat patches, compared to drier ones, and this trend can also be seen in data for *C. nemoralis*. For these species, habitat class explained 21.4–37.3% of the variation in catch.

For *P. oblongopunctatus*, a significant interaction term indicates that the patch-type (islet vs. remnant) effect depended on the habitat type in question (Table 1). Compared to catches of *P. oblongopunctatus* in remnants, it is interesting that islet catches were similar (or even slightly higher) for the dry patches, but for the medium-moist and

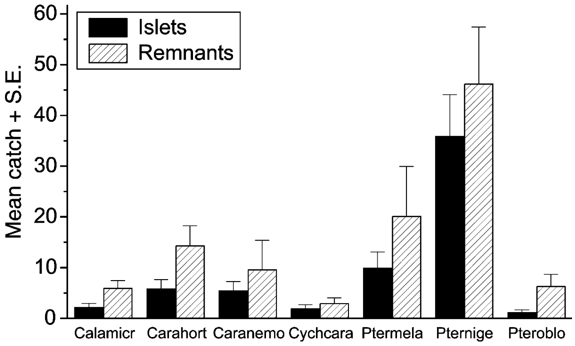

Figure 3. Catches of seven carabid species in the Finnish islets and remnants. Species are indicated with 4 + 4-letter abbreviations; for example, Calamicr = *Calathus micropterus*. For statistical significances, consult Table 1 and Appendix 2.

moist classes the islet catches were clearly lower (Figure 4).

Catches of *C. micropterus* showed a marginally significant trend to decrease with traffic volume, the variable explaining 11.1% of the variation. This effect was rather similar for both islets and remnants, as the slopes (R) between abundance and traffic volume were -0.20 for the islets and -0.55 for the remnants. None of the species tested showed a significant response to time since construction.

Multivariate analyses indicated that the assemblages of islets and remnants were quite similar overall, despite many common species being more numerous in the remnants (Table 1 and Appendix 1). The NMDS (stress 13.97; scatter not shown) scattered scores of both islets and remnants evenly around the origin. The MRT analysis consistently produced a four-node tree that explained 56% of the variation in the data. The tree also consistently had habitat class and traffic volume as the best (and only) explanatory variables for the dichotomies (Figure 5). However, the high cross-validated relative error (0.995) indicated that the produced model has a poor predictive power for a new dataset.

The IndVal calculations were restricted to 11 species with $n > 10$. High indicator values were detected especially for moist patches (habitat class 3), where *C. nemoralis*, *P. melanarius*, *P. niger* and *P. oblongopunctatus* peaked (Figure 5). *C. micropterus*, on the other hand, peaked in dry patches (habitat class 1) with little traffic along the intersection lane. Also *C. hortensis* peaked in dry patches. The first five of these six species are so-called symmetrical indicators (Dufrêne and Legendre 1997), i.e. their presence can be predicted in all patches of the respective mentioned groups of patches. The remaining six species had IndVal between 25 and 55 (asymmetrical indicators), i.e. they contribute to the habitat (patch group) specificity but their presence cannot be predicted for all the patches within the group within which their index value peaked (Dufrêne and Legendre 1997). It is also noteworthy that in terms of species richness and abundance, the drier patches with high traffic volume hosted clearly poorer catches than did the moist patches, and dry patches with less traffic (see the column plots in Figure 5). Generally, however, the plots indicated that most of the abundant species were relatively evenly distributed among the patches.

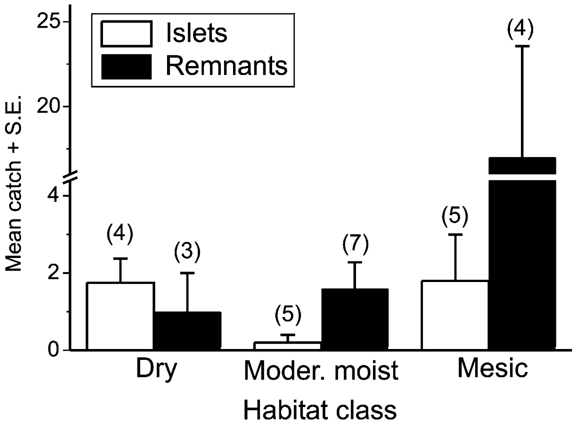

Figure 4. Catches of *Pterostichus oblongopunctatus* in the Finnish islets and remnants, with dry, moderately moist and moist habitats shown separately. Values in parentheses above columns indicate the number of sites falling into each habitat/patch type combination. For statistical significances, consult Table 1 and Appendix 2.

Mark-recapture of carabids adjacent to highway lanes

Six of the ten studied species had recapture rates of 8.4–26.4%, while only 0–3.6% of the remaining species were recaptured (Table 2). With the exception of *P. versicolor* (see below), all recaptured individuals were found on the same side of the highway as they were originally released. Thus, we recorded no highway crossings for these species.

Twenty-two individuals (1.9% of all captures) of marked *P. versicolor* individuals crossed at least one lane (Table 2): 14 individuals moved from the western remnant to the central reservation area, seven moved to the opposite direction, and one crossed the whole highway (from the eastern to the western forest remnant). The average time between release and recapture was 15 (± 12 SD) days for the individuals that crossed lanes, rather similar to the average recapture time lag for the total sample of 225 individuals [14 (± 11 SD) days].

For pooled data from 1993–1994 (Table 3), five species were caught in disproportionately high numbers in the forests, compared to the verges: *Abax parallelepipedus* ($n = 205$, 100% of the captures in the forests), *Calathus rotundicollis* ($n = 43$, 91.5%), *Leistus rufomarginatus* ($n = 210$, 99.5%), *P. oblongopunctatus* ($n = 708$,

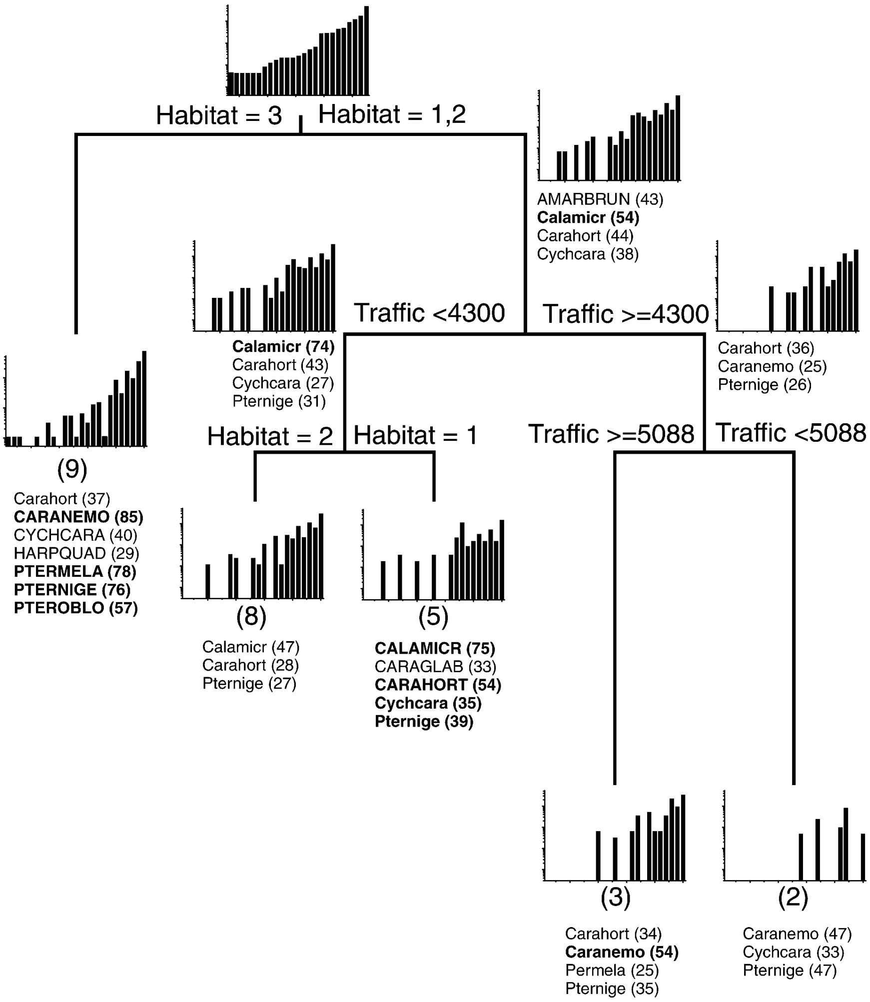

Figure 5. Multivariate Regression Tree for the Finnish data, with species' indicator values (IndVal) calculated for each tree branch. Species are indicated with 4 + 4-letter abbreviations; for example, Calamicr = *Calathus micropterus*. IndVal < 25 were excluded from the graph, values > 50 are shown in bold, and peak value for each species is indicated with capital letters. Column plots show the multivariate species means at each branch (species shown in rank-abundance order of the total catch); note log 10 scale in the *Y*-axes. The number of patches falling into each end node is shown in parentheses. The remnant site of Nummela intersection was excluded because of zero carabid catch and abundant red wood ants.

94.8%), and *Carabus problematicus* (*n* = 209, 89.7%). The treed area was only a narrow strip in the central reservation area, which might force carabids to utilize verges relatively more often than if the treed area was much larger. One might thus expect that the verge captures of these species were mostly in the verges of the central reservation area. However, total catches of carabids other than *P. versicolor* were 251 for the western verge, but only 37 individuals for the two verges of the central reservation strip. *C. nemoralis* and *Nebria brevicollis* showed indications of a generalist life style (46.2 and 66.7% of catches in the forests, respectively), although the latter was significantly more abundant in the forests (Table 3). *P. versicolor* was significantly more abundant in the road verges, compared to the forests.

Discussion

Carabids in small, forested patches that are isolated by roads

Carabid populations and assemblages did not differ markedly between islet and larger remnant

Table 2. Captured and marked carabids at forest and verge sites in 1993–1994 in Nuiler, the Netherlands.

Species	Characteristics[a]			1993		1994			Recaptures (1993)		
	Hab.	Wings	Flight	Forest	Verge	Forest	Verge	Total	Forest	Verge	Cross
Abax parallelepipedus (Pill. and Mitt.)	F	B	n	53	–	263	–	316	14	–	–
Platynus assimilis (Payk.)	F	B	n	12	–	3	–	15	–	–	–
Carabus problematicus Hbst.	F	B	n	85	1	170	23	279	11	–	–
Calathus rotundicollis Dej.	F	D	y	40	2	30	2	74	1	–	–
Leistus rufomarginatus (Dft.)	F	M	?	169	–	255	1	425	6	–	–
Nebria brevicollis (F.)	F	M	y	99	41	90	16	246	9	21	–
Pterostichus oblongopunctatus (F.)	F	M	y	902	17	1179	22	2120	72	5	–
Carabus nemoralis Müll.	G	B	n	56	34	174	127	391	5	7	–
Pterostichus strenuus (Pz.)	G	D	y	4	1	–	1	6	–	–	–
Poecilus versicolor (Sturm)	O	M	y	24	1156	18	268	1466	4	221	22

Recapture events (only for 1993) are shown separately for forest and verge sites, and the number of highway-lane crossing events (Cross) observed.

[a] Species characteristics: Hab. = habitat association (F – forest, G – forest/open-habitat generalist, O – open-habitat species); Wings = wing length (B – brachypterous, D – wing-dimorphic, M – macropterous); Flight = flight observations (n – no, y – yes, ? – tentative evidence for flight capability). According to Den Boer (1977), Van Huizen (1980), Lindroth (1985, 1986, 1992) and Turin et al. (1991).

Table 3. G^2 test with Williams' adjustment for the Dutch carabid data.

Species	Forest[a]	Verge	Expected	G^2_{adj}[b]	df	p
Abax parallelepipedus (Pill. and Mitt.)	205	0	102.5	284.15	1	< 0.001
Platynus assimilis (Payk.)	12	0	6	16.63	1	< 0.001
Carabus problematicus Hbst.	209	24	116.5	168.44	1	< 0.001
Calathus rotundicollis Dej.	43	4	23.5	37.79	1	< 0.001
Leistus rufomarginatus (Dft.)	210	1	105.5	279.77	1	< 0.001
Nebria brevicollis (F.)	114	57	85.5	19.37	1	< 0.001
Pterostichus oblongopunctatus (F.)	708	39	373.5	729.23	1	< 0.001
Carabus nemoralis Müll.	138	161	149.5	1.77	1	ns
Poecilus versicolor (Sturm)	21	1424	722.5	1783.52	1	< 0.001
Sum (G^2)				3320.67	8	< 0.001
Heterogeneity[b]				3320.79	1	< 0.001

Catches adjacent to a highway, viz. forest and verge catches, compared. Data from 1993 and 1994 pooled. Species with expected $n < 5$ were not analyzed.

[a] Three out of six forest samples were randomly chosen to the analysis (as there were only a total of three verge samples).

[b] Heterogeneity was calculated using unadjusted data.

forest patches divided by roads. The most notable difference was reduced catches in islets for all seven species abundant enough for analysis. It is possible that trembling associated with traffic could have direct and indirect effects on carabid behavior and reproductive success leading to reduced populations. Areas close to the highway may also be affected by various chemicals associated with vehicles, control of winter conditions, weed control, etc. and these may have inadvertent effects on carabids. Also micro-climatic conditions typical of forest edges may be unfavorable for forest and generalist species (Murcia 1995), and inter-specific interactions might also contribute to the differences (Loreau 1990, 1992; Niemelä 1993). The observed interaction between patch type and habitat class for *P. oblongopunctatus* indicated that variation in habitat quality (e.g. moisture, shadiness, vegetation) could affect islet populations, in particular. Studies on verge soil quality, its possible effects on microhabitat dimensions, the amount of food, and beetle behavior at habitat edges, might explain the population reductions that we have observed.

We believe that the difference in carabid catches between islets and remnants reflect lower density of populations in the islets, and not simply lower activity. We do not believe that our trapping efforts eliminated beetle populations in any patches during the study. For example, Canadian researchers have pitfall-trapped carabids in three 24 m × 4 m enclosures since 1990 with no apparent trapping-caused effect on beetle abundance (John R. Spence, pers. comm.). Moreover, pitfall-trapping in enclosures placed into a spruce-forest stand showed that *P. oblongopunctatus* density in southern Finnish spruce forests may exceed three individuals/m^2 (Koivula et al. 2003). In the present data, the relative catches (individuals per patch, divided by the forested area of that patch) did not suggest much potential for strong effects of trapping on the sizes of the studied populations, as the peak catches for all species were $< 0.035/\ \mathrm{m}^2$, two orders of magnitude less than what could be reasonably estimated as population size.

We observed that forest carabids, and more marginally, species richness, were predicted by patch type (∼pach size): the remnants produced higher catches than the islets. However, several species, including the majority of forest species, were abundantly caught even in the smallest and longest isolated patches. This finding contrasts with results of Halme and Niemelä (1993), who found that some forest-carabid species were missing from their smallest study fragments. Moreover, we did not detect statistically significant patch-type effects on habitat generalists, whereas Halme and Niemelä (1993) reported that small patches hosted higher generalist catches than did larger patches. These differences may be associated with fine-scale features of the habitats and with land-use history. Halme and Niemelä (1993) sampled forest-interior habitats, whereas we sampled only edge habitats, which should intuitively produce rather poor forest-carabid catches. Furthermore, construction of the studied intersections is rather recent compared to the conversion of large forest tracts into small units surrounded by agricultural and settled areas, which took place hundreds of years ago. It is possible that in our study, carabid populations may have had simply too little time to respond to the decrease in habitat area.

Increasing traffic volume affected negatively the abundance of *C. micropterus* both in the islets and remnants, and the factor was also important in shaping the assemblages of drier trapping sites in MRT. These results may more directly reflect the proximity of urban areas (McDonnell et al. 1997), because urbanization should affect the islets and remnants equally, as the traps were at the same distance from the highway. Indeed, for *C. micropterus* there was no interaction between patch type and traffic volume, and the abundance vs. traffic-volume slope was quite similar for islets and remnants. Traffic volume was not significantly correlated with the distance to Helsinki city centre ($r_s = -0.23$, $p = 0.427$), but it was significantly correlated with the percent cover of utilized (agricultural, settlement and industrial) area, measured from basic maps at 1-km^2 area around each intersection ($r_s = 0.82$, $p < 0.001$). Thus, we hypothesize that the observed decrease in abundance with increasing traffic volume was caused by land-use intensity (the proportion of settlement and industrial vs. forested land) rather than traffic *per se*.

Dispersal and habitat use

We did not find isolation time or traffic volume *per se* important determinants of carabid assemblages in the studied forest patches. Our islet patches may thus host viable relict populations of forest species that cannot – or may not even try to – escape from these very small fragments. The studied species can also have wider habitat use than generally believed. If this is the case, the current classification of carabids into forest and generalist species, based on published habitat associations, may not have been suitable for the study questions here. For example, many boreal forest carabids, such as *C. hortensis* and *C. micropterus*, may thrive in clear-cuts (e.g. Niemelä et al. 1993; Koivula 2002). Also, forest-associated carabids have sometimes – albeit not often – been caught from agricultural fields (Kinnunen 1999; Koivula et al. 2004). These carabids may also benefit from possible negative effects of traffic on potential predators, such as birds and shrews.

Our mark-recapture study showed that at least one open-habitat species moved among isolated patches. However, this result cannot be generalized, as the species can fly, and we did not detect inter-patch movement by forest carabids. Moreover, even some open-habitat specialists may be reluctant to cross highways (see below). Also, if dispersal is (biologically) significant, does it occur from remnant to islet and/or *vice versa*?

Dispersal ability of some carabid species may be good enough for the small patches to receive individuals from surrounding areas, including remnants. Many habitat generalists (and open-habitat species) might be supposed to arrive in the islets by flight. However, of the nine most abundant species in the islets, five were flightless (Lindroth 1985, 1986), and of the captured 385 *P. melanarius* individuals, 9 had long wings, and only one of these was captured in an islet. Thus, if the islets receive generalist immigrants, those that are flightless have to walk across the roadways or arrive from adjacent grassy verges. Carabid highway crossings by foot do occur; for example, Ilpo Rutanen (pers. comm.) observed several flightless *Carabus cancellatus* individuals (try to) cross a two-lane major highway in southern Finland. Also, at least nocturnal species likely disperse during the night time and might succeed, as only ca. 11% of the 24-h traffic volume occurs between 11 P.M. and 7 A.M. (Matti A. Hämäläinen, the Finnish Road Administration, pers. comm.). Furthermore, road verges act as dispersal routes and habitat for many carabids (Mader et al. 1990; Eversham and Telfer 1994; Vermeulen 1994, 1995; Koivula 2003).

To cross or not to cross?

Our mark-recapture data demonstrated that highway crossings by forest-specialist carabids are likely rare events. Similarly, Mader (1984) marked 742 *Abax parallelepipedus* individuals and recorded only one crossing of a highway lane. In the present study, forest carabids also rarely entered the road verge, underlining their strong affinity for forest. The tendency to avoid open sites, in concert with the guiding effect of paved lanes (Mader et al. 1990), makes highway lane crossings by these species unlikely. Moreover, it appears that paved roads even narrower than the Dutch highway that we studied can disrupt gene flow of a flightless forest carabid *Carabus violaceus* (Keller and Largiader 2003).

Also open-habitat specialist carabids may be reluctant to cross highways. In 1990, we carried out another mark-recapture experiment at a highway verge near Apeldoorn, the Netherlands. Despite the weakness of not having the verge transect replicated in this study, the study provided evidence that lane crossings are also rare by carabids specializing in poor sandy habitats. We released a total of 200 *Poecilus lepidus*, 1000 *Harpalus servus* and 275 *Cymindis macularis* individuals at a single point, a few meters from the pavement, and attempted to recapture them in dry pitfall traps placed on the verge 12.5, 25 and 50 m east and 15 m west from the release point. We also had a 4-m wide U-shaped fence touching the asphalt with both of its ends on the other side of the highway, and had four pitfall traps adjacent to it. We recaptured 121 individuals, but none of them had crossed the highway. Moreover, the catches of these carabids were significantly lower at the strip of dense grass, adjacent to the pavement, compared to the more open sandy sections farther away (Mann-Whitney *U*-test for species-specific pair-wise differences; p varied from 0.018 to 0.053). Although vegetation density *per se* may affect such a result, we believe that the interaction of affinity for sandy habitat and the presence of a belt of dense grass adjacent to the pavement acted as an additional dispersal barrier for these stenotopic open-habitat carabids.

Conclusions

The road networks of Finland and the Netherlands have mostly been built within the past 200 years. In 1809, the Finnish network was 11,000 km, while the current length is ca. 380,000 km (Anon. 2003). Similarly, in the Netherlands the network of paved roads was only 450 km in 1904, but has now exceeded 110,000 km (Geesje Veenbaas, the Ministry of Road Works, pers. comm.). These lead to respective road densities 1.3 and 3.2 (km roads/km^2 land area). In the United States, the road network (road density ca. 1) ecologically affects approx. one-fifth of the land area (Forman 2000). If this estimate is generalizable, the road network affects at least 20% of the land area of Finland, and 40–50% of that of the Netherlands. Thus, road construction can surely be a factor of significance in affecting the spatial structure of invertebrate populations.

We have shown that carabid populations, isolated from each other by highways, were significantly affected by patch size, and that forest carabids rarely cross these roads. Our forest–verge comparisons suggest that the barrier effect for forest carabids begins already several meters from the paved lanes, at the forest/verge edge. Nonetheless, we were unable to demonstrate significant effects on carabid abundance or assemblage composition 2–40 years since isolation event. According to Den Boer (1990), an average isolated local population (Den Boer's 'interacting group') of carabids runs an extinction risk of > 50% within 20 years; however, the islets may host more than one local population, and consequently the overall chance of extinction may be lower. Long-term monitoring of populations and individual movements, together with follow-up of reproductive success, would show whether the dynamics of such local populations are independent of each other, and whether isolated islets act as 'sinks' or 'ecological traps' (e.g. Battin 2004) for organisms. Our islet and remnant carabid assemblages were surprisingly similar, considering the often remarkable difference in patch size and the isolation of 2–40 years. This pattern suggests that inter-patch movements – though extremely rare for forest carabids – may retain some similarity, and/or that the habitat quality of islets and remnants has remained nearly equal, thereby maintaining similar assemblage structure for at least a few decades.

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Appendix 1

Appendix 1. Carabids caught from 14 highway intersections in Finland in 2002.

Species	Islets	Remnants	Total
Pterostichus niger (Sch.)	30.93 ± 7.47	43.00 ± 11.25	1035
Pterostichus melanarius Ill.	8.36 ± 2.54	19.14 ± 9.75	385
Carabus hortensis L.	5.07 ± 1.68	11.79 ± 2.56	236
Carabus nemoralis Müll.	4.36 ± 1.43	9.43 ± 5.67	193
Calathus micropterus (Dft.)	2.14 ± 0.69	5.50 ± 1.37	107
Pterostichus oblongopunctatus (F.)	1.07 ± 0.43	6.21 ± 2.31	102
Calathus erratus Sahlbg.	4.43 ± 4.35	0.07 ± 0.00	63
Cychrus caraboides (L.)	1.57 ± 0.53	2.50 ± 0.80	57
Amara brunnea (Gyll.)	0.14 ± 0.68	2.00 ± 0.63	56
Harpalus laevipes Zett.	0.14 ± 0.14	0.86 ± 0.56	14
Carabus glabratus Payk.	0.14 ± 0.10	0.71 ± 0.51	12

Appendix 1. Continued.

Species	Islets	Remnants	Total
Pterostichus strenuus Pz.	0.14 ± 0.10	0.43 ± 0.43	8
Leistus ferrugineus L.	0.21 ± 0.11	0.21 ± 0.11	6
Patrobus atrorufus Strøm	0.07 ± 0.00	0.29 ± 0.16	5
Badister lacertosus Sturm	0.07 ± 0.00	0.21 ± 0.15	4
Leistus terminatus (Hellw. in Pz.)	0.07 ± 0.00	0.21 ± 0.15	4
Pterostichus nigrita Payk.	0.07 ± 0.00	0.21 ± 0.15	4
Calathus melanocephalus L.	0.14 ± 0.00	–	2
Platynus assimilis (Payk.)	0.07 ± 0.00	0.07 ± 0.00	2
Amara eurynota Pz.	–	0.07 ± 0.00	1
Amara lunicollis Schiødte	–	0.07 ± 0.00	1
Carabus granulatus L.	–	0.07 ± 0.00	1
Notiophilus palustris (Dft.)	–	0.07 ± 0.00	1
Stomis pumicatus Pz.	–	0.07 ± 0.00	1
Synuchus vivalis Ill.	–	0.07 ± 0.00	1
Total catch	855	1446	2301
Species richness	19	24	25

'Islets' shows the mean catch ± SE of the islet patches, 'Remnants' shows the mean catch ± SE of the remnant-forest patches. SE values were not calculated for samples <3 individuals (hence SE = 0.00).

Appendix 2

Appendix 2. Details of GLM for the Finnish data; total carabid catch, species richness, and seven abundant species (see text).

Dependent/Model var.	df	MS	*F*	*p*	Tukey's *post hoc*-test
Total catch					
Patch	1	0.26	2.25	0.1522	
Traffic	1	0.08	0.71	0.4126	
Time	1	0.01	0.07	0.7970	
Habitat	2	0.48	4.24	0.0321	(Dry = Moder.) < Moist
Patch × Traffic	1	0.04	0.33	0.5754	
Patch × Time	1	0.04	0.32	0.5795	
Patch × Habitat	2	0.08	0.66	0.5293	
Residuals	17	0.11			
Species richness					
Patch	1	0.07	3.82	0.0672	(Remnant > Islet)
Traffic	1	~ 0.00	~ 0.00	0.9475	
Time	1	~ 0.00	0.09	0.7715	
Habitat	2	0.03	1.62	0.2277	
Patch × Traffic	1	0.01	0.32	0.5791	
Patch × Time	1	~ 0.00	0.12	0.7299	
Patch × Habitat	2	0.03	1.38	0.2777	
Residuals	17	0.02			
C. micropterus					
Patch	1	0.95	7.79	0.0125	Remnant > Islet
Traffic	1	0.51	4.24	0.0553	
Time	1	0.27	2.18	0.1580	
Habitat	2	0.21	1.70	0.2125	
Patch × Traffic	1	0.16	1.28	0.2735	

Appendix 2. Continued.

Dependent/Model var.	df	MS	*F*	*p*	Tukey's *post hoc*-test
Patch × Time	1	~ 0.00	0.02	0.8909	
Patch × Habitat	2	0.14	1.17	0.3336	
Residuals	17	0.12			
C. hortensis					
Patch	1	1.00	3.73	0.0703	(Remnant > Islet)
Traffic	1	0.30	1.12	0.3040	
Time	1	0.03	0.13	0.7274	
Habitat	2	0.01	0.05	0.9499	
Patch × Traffic	1	0.46	1.72	0.2075	
Patch × Time	1	0.16	0.60	0.4503	
Patch × Habitat	2	0.33	1.23	0.3171	
Residuals	17	0.27			
C. nemoralis					
Patch	1	0.01	0.04	0.8473	
Traffic	1	0.03	0.11	0.7472	
Time	1	0.03	0.10	0.7539	
Habitat	2	1.15	4.53	0.0265	((Dry = Moder.) < Moist)
Patch × Traffic	1	0.09	0.34	0.5657	
Patch × Time	1	0.34	1.35	0.2613	
Patch × Habitat	2	0.05	0.18	0.8374	
Residuals	17	0.25			
C. caraboides					
Patch	1	0.16	1.05	0.3205	
Traffic	1	0.01	0.05	0.8291	
Time	1	0.24	1.52	0.2340	
Habitat	2	0.07	0.44	0.6528	
Patch × Traffic	1	0.06	0.41	0.5324	
Patch × Time	1	0.10	0.62	0.4413	
Patch × Habitat	2	0.15	0.96	0.4018	
Residuals	17	0.16			
P. melanarius					
Patch	1	0.18	0.62	0.4425	
Traffic	1	0.27	0.94	0.3471	
Time	1	0.15	0.51	0.4857	
Habitat	2	2.13	7.42	0.0048	(Dry = Moder.) < Moist
Patch × Traffic	1	~ 0.00	~ 0.00	0.9902	
Patch × Time	1	0.31	1.08	0.3124	
Patch × Habitat	2	0.69	2.40	0.1209	
Residuals	17	0.29			
P. niger					
Patch	1	0.05	0.23	0.6408	
Traffic	1	0.19	0.88	0.3604	
Time	1	0.02	0.08	0.7790	
Habitat	2	1.05	4.89	0.0210	(Dry = Moder.) < Moist
Patch × Traffic	1	0.01	0.05	0.8249	
Patch × Time	1	0.14	0.64	0.4358	
Patch × Habitat	2	0.15	0.69	0.5149	
Residuals	17	0.21			
P. oblongopunctatus					
Patch	1	1.22	14.09	0.0016	Remnant > Islet
Traffic	1	0.16	1.89	0.1875	
Time	1	0.02	0.23	0.6354	
Habitat	2	0.54	6.17	0.0097	(Dry = Moder.) < Moist

Appendix 2. Continued.

Dependent/Model var.	df	MS	*F*	*p*	Tukey's *post hoc*-test
Patch × Traffic	1	0.06	0.67	0.4243	
Patch × Time	1	0.09	1.09	0.3106	
Patch × Habitat	2	0.45	5.20	0.0173	
Residuals	17	0.09			

The remnant sample of Nummela intersection was excluded because of its zero total carabid catch and abundant red wood ants. Independent (model) variables are as follows: Patch = patch type (islet vs. remnant), Traffic = traffic volume along the intersection lane that separates islet and remnant, Time = time since intersection construction, and Habitat = habitat class (see text). *Post hoc*-test: 'Remnant > Islet' indicates that the catches were significantly ($p < 0.05$) higher in the remnants, compared to the islets; '(Dry = Moder.) < Moist' indicates that the catches were significantly higher in the moist patches, compared to the dry and moderately moist ones (that were similar, i.e. $p \geq 0.1$). If the *post hoc*-test result is in parentheses with ' > ' or ' < ' symbol, the difference was marginally significant (here, $p < 0.1$).

References

Anon 2003. Road Facts 2003. Finnish Road Administration. Available at http://www.tiehallinto.fi/.

Battin J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18: 1482–1491.

Borg I. and Groenen P. 1997. Modern Multidimensional Scaling: Theory and Applications. Springer-Verlag, New York, 471 pp.

Breiman L., Friedman J.H., Olshen R.A. and Stone C.G. 1998. Classification and Regression Trees. CRC Press, Boca Raton, Florida.

De'ath G. 2002. Multivariate regression trees: a new technique for modeling species–environment relationships. Ecology 83: 1105–1117.

Den Boer P.J. 1977. Dispersal power and survival. Carabids in a cultivated countryside. Miscellaneous Papers Landbouwhogeschool Wageningen 14: 1–190.

Den Boer P.J. 1990. Density limits and survival of local populations in 64 carabid species with different powers of dispersal. Journal of Evolutionary Biology 3: 19–48.

De Vries H.H. 1996. Viability of Ground Beetle Populations in Fragmented Heathlands. Ph.D. thesis, University if Wageningen.

Dickson B.G. and Beier P. 2002. Home-range and habitat selection by adult cougars in Southern California. Journal of Wildlife Management 66: 1235–1245.

Dufrêne M. 1998. Program IndVal. Version 2.0. – Available at http://mrw.wallonie.be/dgme/sibw/outils/indval/home.html.

Dufrêne M. and Legendre P. 1997. Species assemblages and indicator species definition: the need of an asymmetrical and flexible approach. Ecological Monographs 67: 345–366.

Dyer S.J., O'Neill J.P., Wasel S.M. and Boutin S. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Canadian Journal of Zoology 80: 839–845.

Eisto A.-K., Kuitunen M., Lammi A., Saari V., Suhonen J., Syrjäsuo S. and Tikka P.M. 2000. Population persistence and offspring fitness in the rare bellflower *Campanula cervicaria* in relation to population size and habitat quality. Conservation Biology 14: 1413–1421.

Eversham B.C. and Telfer M.C. 1994. Conservation value of roadside verges for stenotopic heathland Carabidae: corridors or refugia? Biodiversity and Conservation 3: 538–545.

Forman R.T.T. 2000. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology 14: 31–35.

Forman R.T.T. and Alexander L.E. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29: 207–231.

Forman R.T.T., Sperling D., Bissonette J.A., Clevenger A.P., Cutshall C.D., Dale V.H., Fahrig L., France R., Goldman C.R., Heanue K., Jones J.A., Swanson F.J., Turrentine T. and Winter T.C. 2003. Road Ecology. Science and Solutions. Island Press, Washington-Covelo-London.

Gloyne C.C. and Clevenger A.P. 2001. Cougar *Puma concolor* use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. Wildlife Biology 7: 117–124.

Halme E. and Niemelä J. 1993. Carabid beetles in fragments of coniferous forest. Annales Zoologici Fennici 30: 17–30.

Hanski I. 1999. Metapopulation Ecology. Oxford University Press, Oxford.

Hourdequin M. 2000. Special section: ecological effects of roads. Conservation Biology 14: 16–17.

Jongman R.H.G., Ter Braak C.J.F. and Van Tongeren O.F.R. 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press.

Keller I. and Largiader C.R. 2003. Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proceedings of the Royal Society of London Series B 270: 417–423.

Kinnunen H. 1999. In Search of Spatial Scale – Carabid Beetle Communities in Agricultural Landscapes. Ph.D. thesis, University of Helsinki.

Koivula M. 2002. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). Forest Ecology and Management 167: 103–121.

Koivula M. 2003. The forest road network – a landscape element affecting the distribution of boreal carabid beetles (Coleoptera, Carabidae). In: Szyszko J., den Boer P.J. and Bauer T. (eds), How to Protect or What We Know about Carabid Beetles. University of Warsaw Press, Warsaw, pp. 287–300.

Koivula M., Hyyryläinen V. and Soininen E. 2004. Carabid beetles (Coleoptera, Carabidae) at forest-farmland edges in southern Finland. Journal of Insect Conservation 8: 297–309.

Koivula M. and Kotze D.J. 2005. Carabid beetles in median strips of three highways around the city of Helsinki, Finland. In: Lövei G. and Toft S. (eds), European Carabidology 2003. Proceedings of the 11th European Carabidologist Meeting. University of Århus, Århus, pp. 151–161.

Koivula M., Kotze D.J., Hiisivuori L. and Rita H. 2003. Pitfall trap efficiency: do trap size, collecting fluid and vegetation structure matter? Entomologica Fennica 14: 1–16.

Legendre P. and Legendre L. 1998. Numerical Ecology, 2nd English ed. Elsevier, Amsterdam.

Lindroth C.H. 1985. The Carabidae (Coleoptera) of Fennoscandia and Denmark, Vol. 15, Part 1. Fauna Entomologica Skandinavica, Leiden, Kopenhagen.

Lindroth C.H. 1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark. Vol. 15, Part 2. Fauna Entomologica Skandinavica, Leiden, Kopenhagen.

Lindroth C.H. 1992. Ground Beetles (Carabidae) of Fennoscandia. A Zoogeographic Study. Part I. Specific Knowledge Regarding the Species. Smithsonian Institution Libraries and The National Science Foundation, Washington DC.

Loehle G. and Li B.L. 1996. Habitat destruction and the extinction debt revisited. Ecological Applications 6: 784–789.

Loreau M. 1990. Competition in a carabid beetle community: a field experiment. Oikos 58: 25–38.

Loreau M. 1992. Species abundance patterns and the structure of ground-beetle communities. Annales Zoologici Fennici 28: 49–56.

Mader H.-J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation 29: 81–96.

Mader H.-J., Schell C. and Kornacker P. 1990. Linear barriers to arthropod movements in the landscape. Biological Conservation 54: 209–222.

McDonnell M.J., Pickett S.T.A., Groffman P., Bohlen P., Pouyat R.V., Zipperer W.C., Parmelee R.W., Carreiro M.M. and Medley K. 1997. Ecosystem processes along an urban-to-rural gradient. Urban Ecosystems 1: 21–36.

Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10: 58–62.

Niemelä J. 1993. Interspecific competition in ground-beetle assemblages (Carabidae): what have we learned? Oikos 66: 325–335.

Niemelä J. and Spence J.R. 1999. Dynamics of local expansion by an introduced species: *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) in Alberta, Canada. Diversity and Distributions 5: 121–127.

Niemelä J., Spence J.R., Langor D.W., Haila Y. and Tukia H. 1993. Logging and boreal ground beetle assemblages on two continents: implications for conservation. In: Gaston K.J., New T.R. and Samways M.J. (eds), Perspectives in Insect Conservation. Intercept Publishers Ltd., Andover, Hampshire, pp. 29–50.

R Development Core Team 2004. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, Available at http://www.R-project.org.

Schøtz-Christensen B. 1965. Biology and population studies of Carabidae of the Corynephoretum. Nat. Jutl. 11: 11–173.

Sokal R.R. and Rohlf F.J. 1995. Biometry: The Principles and Practice of Statistics in Biological Research, 3rd ed. W. H. Freeman and Company, New York.

Thiele H.-U. 1977. Carabid Beetles in their Enviroments. A Study on Habitat Selection by Adaptation in Physiology and Behavior. Zoophysiology and Ecology 10. Springer Verlag, Berlin, 369 pp.

Tilman D., May R.M., Lehman C.L. and Nowak M.A. 1994. Habitat destruction and the extinction debt. Nature (London) 371: 65–66.

Trombulak S.C. and Frissell C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14: 18–30.

Turin H., Alders K., Den Boer P.J., van Essen S., Heijerman T., Laane W. and Penterman E. 1991. Ecological characterization of carabid beetles (Coleoptera, Carabidae) in the Netherlands from thirty years of pitfall sampling. Tijdschr. V. Ent. 134: 279–304.

Van Huizen T.H.P. 1980. Species of Carabidae (Coleoptera) in which the occurrence of dispersal by flight of individuals has been shown. Ent. Ber. 40: 166–168.

Vermeulen H.J.W. 1994. Corridor function of a road verge for dispersal of stenotopic heathland ground beetles Carabidae. Biological Conservation 69: 339–349.

Vermeulen H.J.W. 1995. Road-side Verges: Habitat and Corridor for Carabid Beetles of Poor Sandy and Open Areas. Ph.D. thesis, University of Wageningen.