

Beetles (Coleoptera) in central reservations of three highway roads around the city of Helsinki, Finland

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Central reservations, also known as median strips, are strips of ground, usually paved or landscaped, that divide the carriageways of a highway. We trapped beetles in vegetated central reservations of three Ring Roads around the city of Helsinki, Finland, in 2002, and collected a total of 1512 individuals and 110 species. Ground beetles were the most abundant beetle family collected with 749 individuals and 29 species, followed by rove beetles (410 individuals, 31 species) and weevils (131 individuals, 15 species). Central reservations of the most recently constructed Ring Road II collected significantly more ground-beetle species and rove-beetle individuals than the two older roads (Ring Roads I and III). However, in Ring Road III we collected slightly more weevil individuals, and significantly more individuals of the rest of the beetles. As expected, most species collected were associated with open habitats, eurytopic and capable of flight. Regarding species characteristics, the three roads differed with respect to their catches of short-winged, saprophagous, predator/mixed-diet, small-sized (3.1–6 mm), common and nationally rare species, whereas the occurrences of long-winged, plant-eating, very small (< 3 mm), large (> 6 mm) and moderately common species were more even. Non-metric Multidimensional Scaling demonstrated that the beetle community of the central reservations of Ring Road II was different from the communities of Ring Roads I and III. There appeared to be more within-road variation in community structure at these last two roads. Catches of the nationally vulnerable carabid *Amara equestris*, and several considered rare species, indicate that central reservations have conservation potential.

Introduction

Roads are consequences of human development. With an increase in human mobility, cities and the surrounding landscape are becoming more connected. The ecological effects of roads are

many (Forman *et al.* 2003): roads fragment, isolate and reduce the amount and quality of habitats (Forman & Alexander 1998, Hourdequin 2000, Jaeger & Fahrig 2004); they act as barriers to dispersal (Mader 1984), and consequently act as barriers to gene flow (Keller & Largi-

adèr 2003); they increase mortality of organisms (Trombulak & Frissell 2000, Germaine & Wakeling 2001), and pollute the immediate surroundings (Forman & Alexander 1998). However, roadsides can also act as valuable dispersal routes and/or (temporary) habitats for open-habitat associated species (Vermeulen 1995, Niemelä & Spence 1999, Koivula 2003), especially those requiring dry meadows, as was shown for an endangered plant species in Finland (Eisto *et al.* 2000). Furthermore, some native species may prosper as a result of anthropogenic disturbances along roads. For example, *Acacia* tree recruitment increased alongside roads in New South Wales, Australia, as a result of disturbances from road works (Spooner *et al.* 2004).

Although roadside verges have received some attention in the ecological research, central reservations have been little studied. Central reservations are, usually, artificially-created, narrow habitats situated between highway lanes, as in the present study. As with roadside verges, the vegetation in these strips can be native or exotic and is disturbed repeatedly by mowing, fertiliser enrichment, herbicide and insecticide use, and vehicle related factors (chemical pollution, and litter; Forman & Alexander 1998, Forman *et al.* 2003). Intuitively, these narrow, highly-stressed strips appear to be of little functional or conservation value. Functionally, central reservations are unlikely to aid in the dispersal of species between 'more' suitable habitats in the roadside verges or between meadows. Many species avoid roads (Samways 1994, Charrier *et al.* 1997, Forman *et al.* 2003), and when traffic volume is high, vehicles can cause high mortality. Moreover, in terms of conservation, it is difficult to imagine that these strips will be of use to any species, except the hardiest of generalists (but see Spooner *et al.* 2004).

At time of road construction, the studied central reservations of the three Ring Roads around Helsinki, Finland, consisted of gravel and sand, but some top soil was added later on to promote vegetation growth (J. Karjalainen, Finnish Road Administration, pers. comm.). Thus, the beetle fauna in the central reservations is probably of two origins: individuals introduced with the addition of soil, and/or dispersers from habitats adjacent to the roads. The years following road

construction are likely to have favoured beetle species that are able to adapt to or persist in the harsh conditions in the central reservations, and those species that are good dispersers and colonisers of frequently disturbed, ephemeral habitats. Because Ring Road II was constructed more recently (in 2000) than Ring Roads I and III (constructed from two-lane roads without central reservations to four-lane highways with strips in 1989 and 1978, respectively), we expected the beetle community of the central reservations of Ring Road II to be different in species richness and abundance, and in community composition. Overall, we expected the central reservations to be dominated by highly dispersive, open-habitat generalist species, and that the strips would be of little conservation value.

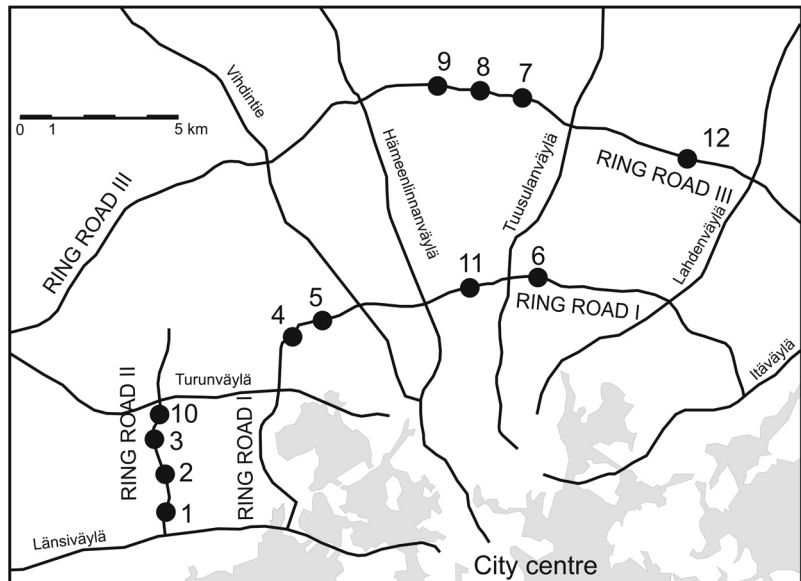
More specifically, we evaluated the potential conservation value to beetles of central reservations of three highway roads (Ring Roads I, II and III) surrounding the city of Helsinki. We collected beetles using pitfall traps, and investigated the following general issues: (1) does the fauna at these three highway strips differ with regard to beetle assemblage structure, abundance and species richness; (2) are highway strips characterised by highly dispersive, open-habitat species; and (3) are these strips of any conservation value?

Material and methods

Beetles were collected in central reservations of three main highways (Ring Roads I, II and III) surrounding the city of Helsinki (Fig. 1). The study sites were 2–4-m wide grassy strips with scarce bushes and trees at some sites (Table 1). Pitfall traps were placed in four sets of 10 traps per Ring Road (Fig. 1), with sets at least 500 m apart. Trapping was continuous from 17 July to 1 October 2002. Beetles were identified using standard keys (Palm 1948–1972, Freude *et al.* 1966–1983, Lindroth 1985, 1986, Hansen 1987, Palm 1996, Gønget 1997). Nomenclature follows Silfverberg (2004).

The beetles collected per 10 traps (i.e. per set) were pooled over the whole sampling period, and analyses were performed at this level. Data were pooled because distances between traps

Fig. 1. The sampling design. Thick lines are major highways and grey on the lower part is the Baltic Sea. Sampling sites (each with 10 pitfall traps) are marked with filled circles, and their numbering corresponds with Table 1.



within a set were too short for individual traps to represent independent replicates (Digweed *et al.* 1995). Also, period-specific catches were sometimes low. Generalised Linear Models were used to test for differences in abundance and species richness in the most specious families (Carabidae, Staphylinidae and Curculionidae), and to test for variation in certain species characteristics (flight ability, body size, food preference and rarity) among the three roads. The following characteristics were taken from the literature: flight ability, body size and food preference (Palm 1948–1972, Freude *et al.* 1966–1983, Lindroth 1985, 1986, 1992, Hansen 1987, Palm 1996, Gønget 1997), and rarity (based on the Frequency-point list of the WWF Finland, where species are ranked on a point system from 1 (common, widespread) to 100 (rare, occasional) based on their national scarcity or finding frequency; Rassi (1993)). These data were modelled following negative binomial error distributions, unless otherwise specified, while species richness data were modelled following Poisson error distributions.

To investigate assemblage-level differences among the three roads, we applied Non-metric Multidimensional Scaling (NMDS; e.g. Borg & Groenen 1997) for the trapping sites by including all the species. We used Bray-Curtis similarity between samples. We also performed a Canoni-

cal Correspondence Analysis (CCA; Jongman *et al.* 1995) on the same dataset using percentage field-, bush- and tree-layer vegetation cover as an environmental dataset. We applied centering by species and Hill's scaling.

Results

In 77 days, we collected 110 beetle species and 1512 individuals in total (Appendix). The three most abundantly collected species were carabids; *Calathus erratus* with 167 individuals (11% of total catch), *Harpalus affinis* (130 individuals, 9%) and *Pterostichus niger* (106 individuals, 7%). These species were followed by *Silpha carinata* (Silphidae; 98 individuals, 6%), the carabid *P. melanarius* (90 individuals, 6%) and the curculionid *Otiorhynchus porcatus* (81 individuals, 5%). The 32 most abundantly collected species represented 90% of the total catch. Regarding species traits (only species with a given trait available in the literature are considered), six out of 104 species (5.8%) were short-winged, and two out of 107 (1.9%) were forest associated. In other words, the majority of beetle species were long-winged or wing dimorphic, with wide habitat tolerance or association to open habitats. In terms of total abundances, long-winged and wing dimorphic species made

Table 1. Vegetation characteristics of the study sites. 'Site (no.)' refers to the name of a given part of the city; the numerical code, used in Fig. 1, is given in parentheses.

Road no.	Site (no.)	Field-layer vegetation		Bush-layer vegetation		Trees (h >1.3 m)	
		Cover (%)	Dominant species (> 5% cover)	Cover (%)	Dominant species	Cover (%)	Species
Ring I	Leppävaara (4)	40	Grasses, <i>Taraxacum</i> Weber, <i>Plantago</i> L., <i>Linaria vulgaris</i> Miller, <i>Achillea ptarmica</i> L.	–	–	–	–
Ring I	Lintuvaara (5)	70	Grasses (esp. <i>Calamagrostis</i> Adanson), <i>Taraxacum</i> Weber, <i>Achillea ptarmica</i> L.	–	–	–	–
Ring I	Pakila (11)	10	Grasses	90	<i>Crataegus</i> L.	35	<i>Ulmus glabra</i> Hudson
Ring I	Pukinmäki (6)	50	Grasses, <i>Vicia</i> L., <i>Potentilla anserina</i> L., <i>Linaria vulgaris</i> Miller, <i>Tussilago farfara</i> L.	–	–	–	–
Ring II	Olari (1)	100	Grasses, <i>Trifolium</i> L., <i>Taraxacum</i> Weber	–	–	–	–
Ring II	Henttaa (2)	80	Grasses, <i>Trifolium</i> L., <i>Taraxacum</i> Weber, <i>Cirsium</i> Miller, <i>Matricaria</i> L.	20	<i>Lonicera caerulea</i> L.	–	–
Ring II	Taavinkylä (3)	80	Grasses, <i>Trifolium</i> L., <i>Taraxacum</i> Weber, <i>Cirsium</i> Miller, <i>Matricaria</i> L.	25	<i>Symphoricarpos albus</i> (L.) S.F. Blake	–	–
Ring II	Turunväylä (10)	50	Grasses, <i>Tussilago farfara</i> L., <i>Artemisia</i> L., <i>Barbarea</i> R. Br.	90	<i>Symphoricarpos albus</i> (L.) S.F. Blake	15	<i>Sorbus intermedia</i> (Ehrh.) Pers.
Ring III	Veromies (7)	100	Grasses, <i>Potentilla anserina</i> L., <i>Achillea ptarmica</i> L., <i>Senecio vulgaris</i> L.	–	–	–	–
Ring III	Ylästö E (8)	90	Grasses, <i>Potentilla anserina</i> L., <i>Achillea ptarmica</i> L.	40	<i>Salix fragilis</i> L. 'Bullata'	–	–
Ring III	Ylästö W (9)	90	Grasses, <i>Potentilla anserina</i> L., <i>Taraxacum</i> Weber, <i>Tussilago farfara</i> L., <i>Achillea ptarmica</i> L.	–	–	–	–
Ring III	Tikkurila (12)	10	Grasses, <i>Trifolium</i> L., <i>Taraxacum</i> Weber, <i>Achillea ptarmica</i> L.	100	<i>Rosa rugosa</i> Thunb.	–	–

up 91.7% of the total catch, and generalists of woodlands and open-habitat together with open-habitat species made up 99.9%.

A slightly higher mean number of carabid individuals was collected from the central reservations of Ring Road II, and this road also collected significantly more carabid species than the other Ring Roads (Table 2 and Fig. 2). For the rove beetles, Ring Road I hosted significantly fewer specimens than Ring Road II, but there was no statistically significant difference in species richness among the three roads. Significantly more weevil and 'the rest of the beetle' individuals were collected from Ring Road III, compared with the other Ring Roads, but their species richness values among the roads were rather even (Table 2 and Fig. 2).

The three roads differed significantly with respect to their number of individuals of short-winged, small bodied (size 3.1–6 mm), saprophagous (= feeding on decaying vegetation matter), and common and rare species (Table 3). Ring Road II hosted more short-winged, saprophagous and common beetles, and slightly more predators, than the other two roads. The staphylinid *Arpedium quadrum* made up 89% of the saprophagous beetle community. On the other hand, central reservations of the oldest highway, Ring Road III, hosted more small (3.1–6 mm) and rare beetles than the other two highways. However, the curculionid *Otiorynchus porcatus*, captured at only one site of Ring Road III, made up 77.9% of the rare species catch at that site, and 35.7% of the total of the rare species catch. The single site thus possibly dominated the analysis. When the GLM for rare beetles was re-run without *O. porcatus*, the difference among roads became non-significant ($p = 0.120$). We detected no statistically significant differences in abundances among roads for long-winged, very small (< 3 mm), large (> 6 mm) or moderately common (frequency points 6–15) species (Table 3).

The NMDS (stress 11.38) revealed that there were considerable differences in the beetle catches among and within the roads (Fig. 3). The central reservations of Ring Road II formed a distinctive and clumped cluster, compared with the strips of Ring Roads I and III that had much more within-road variation, indicated by the widely-scattered site scores. The single sites

Table 2. Model estimates of beetle abundance and species richness at Ring Roads I, II and III in Helsinki, Finland. Response variables are modelled as either negative binomial (carabid, staphylinid and curculionid abundance) or Poisson distributions. For the negative binomial models, θ is an indication of clumping, with a lower value indicating higher clumping. For statistical significances, $^{\circ} = p < 0.10$, $* = p < 0.05$, $** = p < 0.01$ and $*** = p < 0.001$.

Estimate	Carabidae		Staphylinidae		Curculionidae		Rest of the beetles	
	Abundance	Species	Abundance	Species	Abundance	Species	Abundance	Species
Null deviance (df)	15.868 (11)	23.773 (11)	17.229 (11)	12.163 (11)	19.460 (11)	16.486 (11)	167.84 (11)	18.144 (11)
Intercept (SE)	3.917 (0.316)***	1.705 (0.213)***	2.890 (0.323)***	1.872 (0.196)***	1.705 (0.653)**	0.811 (0.333)*	2.225 (0.164)***	1.705 (0.213)***
Ring Road II (SE)	0.597 (0.444)	0.759 (0.258)**	0.944 (0.447) ^o	0.353 (0.256)	-0.693 (0.947)	-0.588 (0.558)	0.396 (0.213) ^o	-0.298 (0.323)
Ring Road III (SE)	-0.094 (0.447)	0.044 (0.298)	0.754 (0.448) ^o	0.353 (0.256)	1.494 (0.903) ^o	0.201 (0.450)	1.257 (0.186)***	-0.319 (0.329)
Residual Deviance (df)	12.871 (9)	11.485 (9)	12.667 (9)	9.638 (9)	13.345 (9)	14.101 (9)	105.27 (9)	17.046 (9)
θ (SE)	2.64 (1.10)		2.77 (1.20)		0.66 (0.29)			

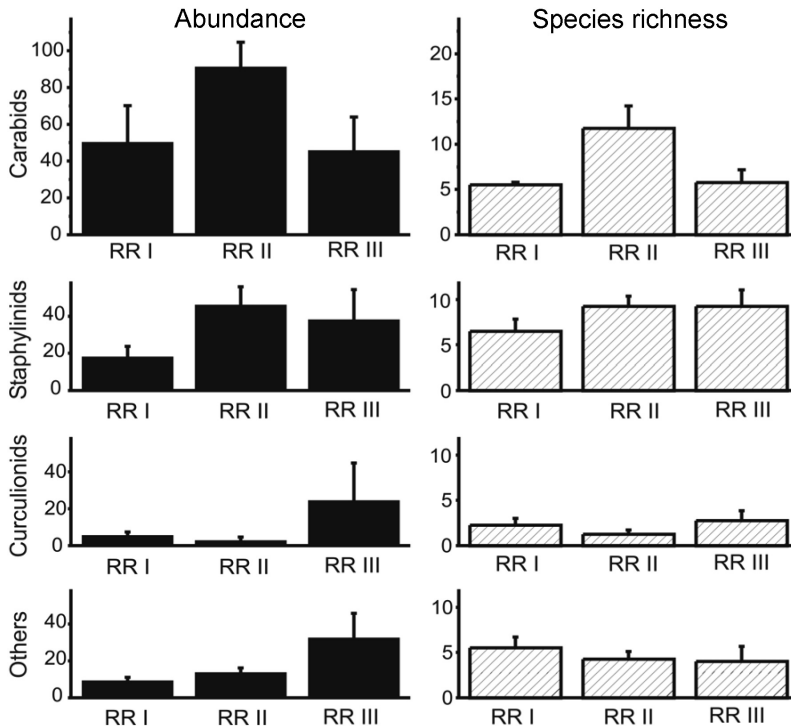


Fig. 2. Abundance (+ SE; left) and species richness (+ SE; right) for carabids, staphylinids, curculionids and other beetles at Ring Roads (RR) I, II and III.

of Ring Roads I and III, located at the extreme bottom area on the graph represent the two poorest sites with total catch/species richness of 31/14 and 14/6, respectively. For all the other sites, the total catch varied from 88 to 244 individuals and from 16 to 33 species.

As is evident from the Appendix and the NMDS plot (Fig. 3), some species were associated with certain Ring Road central reservations. For example, according to the Appendix, the carabid *Pterostichus melanarius* and the staphylinid *Philonthus cognatus* were collected abundantly in central reservations of Ring Road II, but only occasionally at Ring Roads I or III. So too were *P. niger*, *Harpalus rufipes* and *Trechus quadristriatus*. Examples of other species showing an association to a particular Ring Road included *Harpalus affinis* (Ring Road I), *Silpha carinata* (Ring Road III), *Amara bifrons* and *Calathus erratus* (both Ring Roads I and III) and *Trixagus carinifrons* (Ring Roads I and II).

In the CCA, the percentage cover of vegetation did not explain the catches statistically significantly, although field- and bush-layer vegetation together explained 21.1% of the variation in the beetle data, and 75.9% of the species-environment relationship (results not shown). The three environmental variables did not correlate much with each other (variance inflation factor values 1.73–2.70).

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Discussion

This study demonstrated that several beetle species appear to be abundant in the severe environment of central reservations. *Amara equestris*, a carabid vulnerable in Finland (Rassi et al. 2000), was quite abundant at one site. Also, several other beetles, considered to be rare in Finland, were abundant, e.g. the curculionid *Otiorhynchus porcatus* (81 individuals) and the staphylinid *Tachinus marginatus* (66). Moreover, both *A. equestris* and *O. porcatus* were collected only from the oldest Ring Road, and *T. marginatus* was most abundant there. In the Netherlands, Vermeulen et al. (1994) collected several geographically restricted or rare carabid species at roadside verges. These and the present results indicate that both verges and central reservations have conservation potential. Not surprisingly, the majority of beetle species collected were

Table 3. Model estimates for beetle life-history characteristics at Ring Roads I, II and III in Helsinki, Finland. Response variables are modelled as either negative binomial or Poisson (short-winged beetles) distributions. For the negative binomial models, θ is an indication of clumping, with a lower value indicating higher clumping. For statistical significances, $^{\circ} = p < 0.10$, $* = p < 0.05$, $** = p < 0.01$ and $*** = p < 0.001$.

Estimate	Wing length				Body size (mm)			
	Short-winged	Long-winged	1–3	3.1–6	6.1–9	> 9		
Null dev. (df)	132.057 (11)	14.232 (11)	19.65 (11)	17.244 (11)	13.192 (11)	15.543 (11)		
Intercept (SE)	1.099 (0.289)***	4.382 (0.297)***	1.946 (0.421)***	2.862 (0.464)***	2.526 (0.365)***	3.744 (0.331)***		
RR II (SE)	2.120 (0.306)***	0.478 (0.419)	0.496 (0.583)	0.707 (0.651)	-0.329 (0.524)	0.762 (0.465)		
RR III (SE)	0.223 (0.387)	0.369 (0.419)	-0.934 (0.640)	1.113 (0.650) ^o	-0.151 (0.520)	0.461 (0.466)		
Residual dev. (df)	21.519 (9)	12.860 (9)	14.54 (9)	14.430 (9)	12.800 (9)	12.911 (9)		
θ (SE)		2.94 (1.21)	1.77 (1.04)	1.24 (0.53)	2.21 (1.09)	2.42 (0.99)		
Estimate	Food			Frequency (points)				
	Plant	Predator/mixed diet	Saprophagous	1–5	6–15	> 15		
Null dev. (df)	18.894 (11)	16.708 (11)	19.306 (11)	18.763 (11)	15.329 (11)	22.596 (11)		
Intercept (SE)	2.848 (0.471)***	4.082 (0.290)***	0.223 (0.623)	3.720 (0.249)***	3.376 (0.431)***	2.140 (0.506)***		
RR II (SE)	-0.651 (0.676)	0.724 (0.407) ^o	1.792 (0.781)*	0.810 (0.347)*	0.480 (0.606)	-0.268 (0.722)		
RR III (SE)	0.822 (0.660)	0.089 (0.407)	0.693 (0.822)	0.202 (0.350)	0.350 (0.607)	1.592 (0.699)*		
Residual dev. (df)	14.047 (9)	12.726 (9)	13.229 (9)	12.573 (9)	14.685 (9)	13.719 (9)		
θ (SE)	1.20 (0.52)	3.13 (1.30)	1.33 (0.86)	4.47 (1.96)	1.41 (0.62)	1.10 (0.48)		

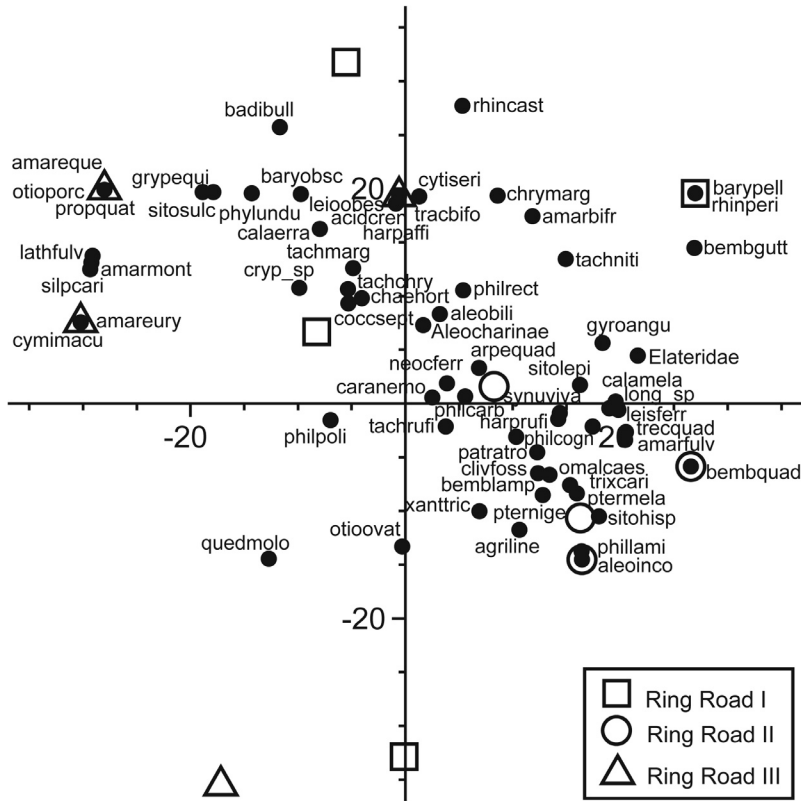


Fig. 3. Non-metric Multi-dimensional Scaling for beetles caught at Ring Roads I, II and III. Singletons are not presented here. Scores of species are indicated with 4 + 4 letter abbreviations; for example, bembgutt = *Bembidion guttula*.

eurytopic, long-winged (thus probably capable of flight) and associated with open habitats. In terms of carabid beetles, 20 of the 29 carabid species collected here are classified as either synanthropic or occurring in human-altered habitat such as parks, towns or agricultural land (Lindroth 1985, 1986, 1992).

The slightly higher abundance of small beetles at Ring Road II, as compared with that at the other two roads, can be explained by the fact that the majority of small carabids in the data were long-winged; 36 out of 37 species and 336 out of 340 specimens were both small (3.1–6 mm) and had long wings (Pearson correlation: d.f. = 12, $r = 0.71$, $p = 0.010$). We also detected a significant difference in saprophagous beetle abundance among the roads. *Arpedium quadrum* dominated the analysis (see Results) and was primarily collected from sites at Ring Road II. This species is associated with decaying plant material and wet places, but apart from the fact that the central reservations of Ring Road II are considerably younger than those of the other two

roads, we do not have an explanation for this species' abundance there.

The beetle community in central reservations of Ring Road II differed considerably from those of Ring Roads I and III, forming a slightly distinct scatter with site scores much more aggregated than in the latter two roads. We suggest that the more recent road construction and associated human-caused introductions of beetles play a role here. In the older Ring Roads I and III, some species may have disappeared from the central reservations because these sites may be hostile habitats (because of frequent disturbances like mowing and traffic-related pollution), the microhabitat has changed along the vegetation succession, and/or the patches are too small for them to persist there. Consequently, some species may not be able to maintain viable populations there.

Our analyses of species characteristics indicated that flightless (and consequently potentially poorly disturbance adapted; Den Boer (1981, 1985)) beetles were more abundant at central reservations of Ring Road II than at the

other two roads. Following the construction of central reservations, the assemblage may host beetles typical of the habitat where the added top soil was taken from. Later on, in concert with vegetation succession, the beetle community may adjust towards relatively more disturbance-tolerant species. Some species characteristic of relatively open and dry meadow-like conditions may persist there, as was shown by the high overall catches of the rare staphylinid *Tachinus marginatus*.

Human-aided introductions of species, followed by extinctions, may not be the only reason why Ring Road II is different from the two older highways, because Ring Road I — constructed in 1989 — had fewer species and individuals than the oldest Ring Road III (constructed in 1978). An additional possibility is a difference in the amount and quality of adjacent habitats along the three roads, thus enabling varying numbers and types of species to colonise the strips. Indeed, Ring Road II had very wide grassy verges and large meadows adjacent to the road, while Ring Roads I and III had narrower verges, and the adjacent habitat was dense deciduous forest, settlements or industrial areas. The species pools of the roadside verges clearly need to be studied in relation to the beetles in the central reservations.

Is crossing a big road a likely event? Some carabids occasionally cross paved roads (Mader 1984), and crossing is obviously easier for species capable of flight. Crossing by non-fliers can actually be a common phenomenon: during an early summer morning, Ilpo Rutanen (pers. comm.) observed several *Carabus cancellatus* Ill. individuals (trying to) cross a 10-m wide, two-lane paved main highway in southern Finland. Furthermore, at least several carabid species are active at night (Lindroth 1985, 1986, Lövei & Sunderland 1996), when there is less traffic, and beetles trying to cross roads may suffer lower mortality from passing cars (see Jaeger & Fahrig 2004). At our study sites, for example, the average traffic volume varies between 40 000 and 80 000 vehicles/24 hours, but only ca. 11% of the daily traffic is between 22:00 and 7:00 (data from the Finnish Road Administration).

However, even though beetle individuals can travel relatively long distances by walking (Thiele 1977, Den Boer 1981) and theoretically

can cross these roads, dispersing individuals may avoid crossing inhospitable habitat such as roads, and prefer to disperse along roadside verges or hedgerows (Vermeulen 1995, Charrier *et al.* 1997, Petit & Burel 1998). Mark-recapture sampling at verges and central reservations would shed more light on how isolated the central reservations actually are.

Conclusions

Although road-effect reviews and studies often emphasise the negative effects of road construction (e.g. Forman & Alexander 1998), we point out that roadsides and central reservations may also be valuable habitat for rare and threatened species (see Eversham *et al.* 1996). The beetle communities of the central reservations around Helsinki were species rich, and included rare species. It is likely that these areas are even richer in beetle species because our sampling period did not include the whole activity period or multiple years, and uncommon species are usually only collected with intensive sampling. With careful management, these sites may act at least as stepping stones and temporary habitat for species associated with some habitats that are currently scarce in Finland, for example dry meadows of semi-agricultural landscapes. Currently, the strips are managed only by mowing twice a summer and, at sites with recently planted ornamental bushes, by using herbicides with levels lower than farmland use (A. Kärkkäinen, Finnish Road Administration, pers. comm.). So, should these potentially 'sink' or 'ecological trap' habitats be improved for the benefit of indigenous species? Favouring native meadow herbs and preventing densely-growing generalist grasses from smothering these plants (i.e. maintaining high vegetation diversity) in the strips and verges will make them more suitable for open-habitat beetles and other invertebrates.

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Appendix. Beetles collected from the median grass strips of Ring Roads I, II and III in 2002 in Helsinki, Finland. Families are in taxonomic order and species within each family in alphabetical order. Nomenclature follows Silfverberg (2004).

Species	Ring road			Species	Ring road		
	I	II	III		I	II	III
Carabidae				Leiodidae			
<i>Amara apricaria</i>	–	1	–	<i>Hydnobius spinipes</i>	–	–	1
<i>A. aulica</i>	–	1	–	<i>Leiodes obesa</i>	–	–	6
<i>A. bifrons</i>	31	1	15	Silphidae			
<i>A. equestris</i>	–	–	11	<i>Silpha carinata</i>	–	–	98
<i>A. eurynota</i>	–	–	6	Staphylinidae			
<i>A. fulva</i>	–	3	–	<i>Acidota crenata</i>	–	–	2
<i>A. montivaga</i>	–	–	10	<i>Aleochara bilineata</i>	15	14	12
<i>A. municipalis</i>	–	1	–	<i>A. inconspicua</i>	–	3	–
<i>Badister bullatus</i>	3	–	1	<i>Anotylus rugosus</i>	–	–	1
<i>Bembidion bruxellense</i>	–	1	–	<i>Arpedium quadrum</i>	1	29	10
<i>B. guttula</i>	–	2	–	<i>Bisnius cephalotes</i>	1	–	–
<i>B. lampros</i>	–	2	–	<i>Carpelimus bilineatus</i>	–	1	–
<i>B. quadrimaculatum</i>	4	1	–	<i>Deleaster dichrous</i>	–	–	1
<i>Calathus erratus</i>	50	16	101	<i>Drusilla canaliculata</i>	–	–	1
<i>C. melanocephalus</i>	1	3	–	<i>Gabrius astutoides</i>	–	–	1
<i>Carabus nemoralis</i>	2	2	2	<i>Gyrohypnus angustatus</i>	7	5	–
<i>Clivina fossor</i>	–	2	–	<i>Lathrobium brunnipes</i>	–	–	1
<i>Cymindis angularis</i>	–	–	1	<i>L. fulvipenne</i>	–	–	2
<i>C. macularis</i>	–	–	2	<i>Ocypus brunnipes</i>	–	–	1
<i>Harpalus affinis</i>	84	27	19	<i>Omalium caesum</i>	2	–	–
<i>H. rufipes</i>	10	59	1	<i>Philonthus carbonarius</i>	–	5	6
<i>Leistus ferrugineus</i>	–	2	–	<i>P. cognatus</i>	2	33	6
<i>Patrobus atrorufus</i>	–	5	1	<i>P. laminatus</i>	–	5	–
<i>Pterostichus crenatus</i>	–	1	–	<i>P. politus</i>	–	1	1
<i>P. melanarius</i>	5	85	–	<i>P. rectangulus</i>	1	1	–
<i>P. niger</i>	6	91	9	<i>Quedius molochinus</i>	1	–	1
<i>Synuchus vivalis</i>	–	3	–	<i>Staphylinus erythropterus</i>	–	1	–
<i>Trechus quadristriatus</i>	5	56	3	<i>Stenus biguttatus</i>	1	–	–
<i>T. rivularis</i>	–	–	1	<i>Tachinus laticollis</i>	1	–	–
Hydrophilidae				<i>T. marginatus</i>	10	9	47
<i>Cryptopleuron subtile</i>	1	–	–	<i>T. rufipes</i>	–	4	1
<i>Hydrobius fuscipes</i>	1	–	–	<i>Tachyporus chrysomelinus</i>	5	9	20
				<i>T. hypnorum</i>	–	–	1

Continued

Appendix. Continued.

Species	Ring road			Species	Ring road		
	I	II	III		I	II	III
<i>T. nitidulus</i>	5	3	2	Cerambycidae			
<i>Xantholinus tricolor</i>	7	36	9	<i>Anoplodera rubra</i>	–	1	–
Aleocharinae spp.	13	26	27	Chrysomelidae			
Scarabaeidae				<i>Chaetocnema hortensis</i>	1	2	2
<i>Serica brunnea</i>	1	–	–	<i>Chrysolina marginata</i>	2	–	4
Byrrhidae				<i>Longitarsus succineus</i>	–	–	1
<i>Cytilus sericeus</i>	3	–	5	<i>L. kutscherai</i>	–	1	–
Heteroceridae				<i>L. nasturtii</i>	–	1	–
<i>Heterocerus fenestratus</i>	–	1	–	<i>L. spp.</i>	1	2	–
Throscidae				<i>Neocrepidodera ferruginea</i>	6	3	–
<i>Trixagus carinifrons</i>	7	31	–	<i>Phyllotreta undulata</i>	–	–	2
Elateridae				Apionidae			
<i>Agriotes lineatus</i>	–	7	1	<i>Apion haematodes</i>	–	–	1
<i>Hemicrepidius niger</i>	1	–	–	<i>A. gibbirostre</i>	–	1	–
<i>Hypnoidus riparius</i>	–	1	–	<i>A. seniculus</i>	1	–	–
Nitidulidae				Curculionidae			
<i>Eपुरaea aestiva</i>	–	1	–	<i>Barynotus obscurus</i>	–	–	3
<i>Meligethes aeneus</i>	1	–	–	<i>Barypeithes pellucidus</i>	4	–	–
<i>Omosita depressa</i>	1	–	–	<i>Ceutorhynchus obstrictus</i>	–	–	1
Cryptophagidae				<i>C. punctiger</i>	–	–	1
<i>Cryptophagus</i> spp.	–	1	1	<i>Grypus equiseti</i>	–	–	3
<i>Atomaria</i> spp.	–	–	1	<i>Otiorhynchus ovatus</i>	5	–	3
Coccinellidae				<i>O. porcatus</i>	–	–	81
<i>Adalia bipunctata</i>	1	–	–	<i>Rhinoncus castor</i>	6	–	–
<i>Coccinella septempunctata</i>	8	1	2	<i>R. pericarpus</i>	2	–	–
<i>Hippodamia tredecimpunctata</i>	–	–	1	<i>Sitona hispidulus</i>	–	6	–
<i>Propylaea quattuordecimpunctata</i>	–	–	3	<i>S. lateralis</i>	1	–	–
Latrididae				<i>S. lepidus</i>	3	5	–
spp.	1	1	–	<i>S. sulcifrons</i>	1	–	1
Lagriidae				<i>S. suturalis</i>	–	–	1
<i>Lagria hirta</i>	–	–	1	<i>Trachyphloeus bifoveolatus</i>	–	–	4