

# Roadside habitats: effects on diversity and composition of plant, arthropod, and small mammal communities

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**Abstract** Road edge effects cover extensive areas and exert a wide range of ecological influences on nearby plants and animals. Most studies have focused on individual and population level effects of the road edge; less is known about how communities and their functionality are altered in proximity to roads. Here, we studied the effect of road edges on species richness, rarity, endemism, composition, and functional (trophic) classification of communities of plants, ground-dwelling arthropods (beetles, spiders, scorpions, diplopods), and small mammals. The study, conducted in a Mediterranean ecosystem in central Israel, included sampling of these taxa in 10 plots adjacent to a regional road, and in 12 nearby control plots located in a typical shrubland habitat. We found a variety of community level road edge effects on the structure, composition, and function of the studied communities. The extent of effects varied among taxa, but they were generally positive or neutral. For the species-rich taxa (plants, beetles, and spiders), distinct road edge communities characterized by higher richness and altered species composition were found. Rarity and endemism were lower, and the proportion of disturbance-associated plant species was higher at the road edge. Among the species-poor taxa, scorpions and small mammals were more abundant along road edges than in control plots, while diplopods, the only negatively affected taxon, showed decreased abundance along the road. No ecologically meaningful changes in richness or composition were detected for the species-poor taxa along the road edge. Road edges profoundly affect floral and faunal communities, with possible implications for biodiversity conservation.

**Keywords** Biodiversity · Beetles · Diplopods · Road edge effect · Scorpions · Spiders

## Introduction

Edge effects, occurring at the boundary of two contrasting habitats over which significant ecological effects can be detected (Murcia 1995), greatly affect habitat quality and

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connectivity, the dynamics of populations and communities, and, ultimately, the persistence of species in fragmented landscapes (Ries et al. 2004; Ewers and Didham 2008; Gillies and St. Clair 2010; Zurita et al. 2012). The great extent of areas affected by fragmentation and edge effects (Vitousek et al. 1997) and their possible synergistic interactions with other extinction drivers make edge effects a major conservation concern worldwide (Brook et al. 2008). Road edges are particularly significant both in their spatial extent and in their ecological effects, at scales ranging from local to global. About 20 % of the US land area is estimated to be influenced by roads, and a similar situation likely exists in many more western countries (Forman 2000; Riitters and Wickham 2003). Besides the vast extent of land they cover, road edge habitats, defined as the area adjacent to the road over which significant edge effects are measured (Forman and Alexander 1998), constitute a transition zone that may buffer some of the ecological effects caused by roads and may thus be targeted for specific management and mitigation actions (Roedenbeck et al. 2007). In order to fully evaluate the ecological effects of roads and their associated edge habitat, it is necessary to gain a broad perspective on how whole communities and functional guilds are affected. Most studies, however, focus on the effects of road edge habitats on individuals and populations, while limited attention has been directed at changes in diversity and composition of whole communities inhabiting road edge habitats (van der Ree et al. 2011).

Roads have considerable and diverse ecological effects at different spatial scales (as reviewed by Forman and Alexander 1998; Jones et al. 2000; Trombulak and Frissell 2000; Fahrig and Rytwinski 2009). On wide spatial scales, roads are among the main causes of loss and fragmentation of habitats in many regions (Reed et al. 1996; Bhattacharya et al. 2003; Hawbaker and Radeloff 2004). On a local scale, the considerable ecological effect of roads may result from direct mortality caused by construction operations or car collisions or, more importantly, by changes in habitat conditions along road edges (Forman and Alexander 1998). Road edges display a variety of physical and chemical changes as a result of road operation and traffic (Forman et al. 2002; Delgado et al. 2007; Parris and Schneider 2008; Hoskin and Goosem 2010) road edges are characterized by altered micro-climatic conditions, hydrology regimes and soil composition and density, and increased levels of noise, light, and pollutants in the air, soil and water. Roads constitute a partial to complete barrier for movement of many organisms, depending on the mobility and behavior of taxa and on road characteristics (Jaeger and Fahrig 2004). Roads induce changes in faunal behavior and physiology which affect factors such as foraging, territory ranges, reproductive success, and survival rates (Spellerberg 1998). These changes are caused by either attraction to, or avoidance of the road and its vicinity (Fahrig and Rytwinski 2009), and may have significant demographic and genetic consequences (Jackson and Fahrig 2011). Moreover, roads contribute to the introduction and spread of exotic species to adjacent natural areas (evidence exists mostly for plants Gelbard and Belnap 2003; Song et al. 2005; Fowler et al. 2008), and alter the composition of nearby communities (Pauchard and Alaback 2004; Prasad 2009).

Recent years have brought increased interest in the ecological significance of the edge effects of roads and the need to better mitigate them (Hourdequin 2000; van der Ree et al. 2011). However, little attention has been directed towards examining the road edge habitat from a broad perspective of community level effects synthesized over a range of different taxa of diverse phylogenies and functionality (van der Ree et al. 2011). This study aims to investigate the structure and composition of plant, ground dwelling arthropod, and small mammal communities in a road edge habitat, in comparison with communities in a nearby natural area, in order to gain insight into community level effects of the road edge and the

ecological functioning of these communities. We hypothesize that the compositional differences between the communities found along the road edge compared to those in the nearby natural area will be greater than the average differences found within each of these communities. This investigation will also provide insight into the sensitivity of the studied taxa to changes in land-use and habitat conditions, and thus their suitability as indicators of community level changes caused by development.

## Materials and methods

### Study system

The research was conducted in the Jerusalem mountains and the Judean foothills, ~30 km southwest of Jerusalem. The region is characterized by Mediterranean-type vegetation bordering an arid ecosystem to the south (Weizel et al. 1978), and has high faunal and floral diversity and endemism (Yom-Tov and Tchernov 1988). We worked along a regional 2-lane road (route 38 from Beit Shemesh to Beit Guvrin) with intermediate traffic loads (average traffic loads in 2006–2011: 7,200–10,200 vehicles/day; Israel Central Bureau of Statistics 2012). Parts of this road transect an open landscape of Mediterranean shrubland (garigue) typical of the region. These parts were thus considered a bottle-neck in the national ecological corridor network of Israel (Israel Nature and Parks Authority 2008). In these areas, we established 10 “road edge plots” measuring 1,000 m<sup>2</sup> (50 × 20 m), 5 on each side of the road. Plot size was based on the necessary sampling effort for plants (measured by area sampled) determined in a preliminary study (Mandelik et al. 2002). Plots were parallel to the road and extended 20 m into the adjacent shrubland starting from ca. 2 m from the bare unpaved shoulder bordering the road on each side. Distances between adjacent plots were 150–600 m, minimizing the possibility of spatial autocorrelation and pseudo-replication (Digweed et al. 1995).

We established 12 control plots of the same size and shape as the road edge plots, 6 on each side of the transected shrubland at distances of 550–1,700 m from the road. In order to account for environmental variability in the studied landscape, caused mainly by variation in perennial vegetation cover (Mandelik et al. 2012), the location of the control plots was chosen to represent both sparse and dense shrubland configurations typical of the region (Mandelik 2005). Distances between adjacent control plots were 150–450 m. We found limited spatial auto-correlation between the control plots and the road edge plots in species composition of the studied taxa (see preliminary analyses).

In addition to roads, major disturbances in the region include grazing, fire, agriculture, and settlements. All plots were at least 500 m from a recently burnt area (<4 years), cultivated area, or settlements. Since grazing occurs throughout the region and could not be avoided, we incorporated it into our sampling design. All our plots were subject to a similar level of low intensity cattle grazing, confirmed by a survey of cattle dung density conducted in all plots at the end of the study (Mandelik 2005).

### Sampling of flora, fauna, and environmental structure

We sampled six taxa: vascular plants, ground-dwelling beetles, spiders (mostly ground-dwelling), scorpions, diplopods, and small mammals. Based on the number of species sampled in each taxon, we classified them as species-rich taxa (plants, beetles and spiders) and species-poor taxa (scorpions, diplopods, and small mammals). We established the

sampling effort required for the faunal and floral surveys in a preliminary study using species accumulation curves (see Mandelik et al. 2002).

We recorded vascular plant species in each plot along four 50-m 1-m wide transects, 5 m apart. Additional time was spent walking haphazardly in the plot recording new species encountered until no new species were found for 5 consecutive minutes (species accumulation curves level off after 5 min; Mandelik 2005). We additionally recorded the abundance (ground cover) of the dominant plant species (>1 % ground cover; see details below). We sampled vascular plants twice: once in March (early spring) and once in May (late spring).

We sampled arthropods (beetles, spiders, scorpions, diplopods) with pitfall traps, 10 cm in diameter and 10 cm in depth, filled with ~100 ml of ethylene glycol to prevent predation and decomposition of specimens. In each plot, 12 pitfall traps were buried flush with the ground surface in a 10 × 17 m grid. To decrease bias in pitfall trap catches due to microhabitat structure, we matched ground cover as much as possible in a 2 m-diameter area around each trap and made sure no prominent obstacles such as large rocks or tree trunks were present. We conducted five 1 week sampling sessions, one each in August, November, January, March and late May. All collected specimens were deposited in the National Collections of Natural History at the Tel Aviv University Zoological Museum.

We sampled rodents with 12 Sherman traps per plot in the same grid used for the pitfall traps. We conducted three sampling sessions during the period of August–November, corresponding to peak population levels. In each session, sampling was conducted for one night, from evening to the next morning, during the first quarter of the moon cycle so as to standardize conditions and increase trapping efficiency. Individuals were identified to species and released. As there is no reason to assume differences in re-capture rates among plots, we used trapping data to calculate relative abundances and diversity measures.

In each plot we recorded detailed measures of environmental structure in four 10 × 10 m quadrats randomly located within the plot. If strong patchiness in physical structure of the vegetation or substrates was evident, quadrats were located accordingly. In each quadrat we recorded altitude, slope, aspect (in degrees), ground cover by vegetation (overall, and separately for the dominant species providing >1 % cover; visual estimation), ground cover by substrates (bare ground, stones and rocks; visual estimation), and vertical vegetation profile (layering, represented by the relative cover of plant life forms i.e. annuals, semi-shrubs, shrubs, trees; visual estimation) (see detailed description of sampling methods in Mandelik et al. 2012). We additionally evaluated the complexity of the ground habitat and of the layering using the Simpson index on the different cover types and their relative abundances (Naveh and Whittaker 1979).

#### Rarity, endemism and trophic classification

We determined species rarity and endemism only for the species-rich taxa, as the small numbers of species in the other taxa limit statistical analysis. Rarity assessments were based on the relative abundance of each species in the present study; rare species were classified as those in the first quartile of the distribution (Gaston 1994). Plant species endemic to the Levant region including Lebanon, Syria, Jordan and Israel were determined according to Fragman et al. (1999); beetles were identified according to the National Collections of Natural History at the Tel Aviv University Zoological Museum. Due to limited ecological knowledge, we were unable to determine endemism of the spider community. We additionally classified plant species known to be associated with disturbed

habitats such as built-up areas, road edges and inactive crop-land following Feinbrun-Dothan and Danin (1998).

We classified the beetle community into three trophic guilds: herbivores, predators, and decomposers (saprophytes). We further divided decomposers into those foraging on decomposing plants and those foraging on decomposing carrion and dung. Trophic classification is according to the adult stage and was based on data from the National Collections of Natural History at the Tel Aviv University Zoological Museum.

### Preliminary analyses

Since distances between plots were variable, we explored the possible spatial autocorrelation in species assemblages between plots. We used a Mantel test (Mantel; PC-ORD version 5, MjM Software, Gleneden Beach, Oregon) to determine the correlation between geographic distance (calculated with ArcGIS 9.2, Environmental Systems Research Institute, Redlands, California) and a species' similarity matrix for each taxon (using the relative Sorensen similarity index; Magurran 2004) for all pairs of plots. Spatial autocorrelations accounted for up to 10 % of the variation in species composition in the control and the road edge plots (9,999 randomizations; control plots:  $r^2 = 0.0009\text{--}0.101$ ; road edge plots:  $r^2 = 0.0004\text{--}0.09$ ). Thus, spatial autocorrelation is of limited ecological significance in this study system and we did not include geographic distances between plots in further analyses.

Some pitfall traps were damaged by animal trampling, fallen branches, or other disturbances. We therefore used a log-linear model to check the equivalency in actual sampling effort [i.e. number of undamaged traps (response variable) between road edge and control plots in each sampling round (explanatory variables)]. The average cumulative number of undamaged traps in 10 out of 12 control plots was estimated using 1,000 bootstrap simulations. Significant differences in the number of undamaged pitfall traps were found between sampling periods but not between plot types (sampling periods:  $\chi^2 = 32.3$ ,  $df = 4$ ,  $p < 0.001$ ; plot type:  $\chi^2 = 0.13$ ,  $df = 1$ ,  $p = 0.72$ ). Thus, actual sampling effort was similar between the control and road edge plots and we could compare them directly.

The physical heterogeneity of the studied landscape made it necessary to check for possible differences in habitat structure between the road edge and the control plots. We conducted a principal component analysis (PCA; Canoco for Windows 4.5, Microcomputer Power, Ithaca, NY) on the environmental variables described above to extract main environmental variation axes while accounting for inherently interconnected multiple variables, e.g. % ground cover by different substrate types. To achieve normal distributions ground and vertical cover variables were arcsine transformed; altitude, aspect, and slope were square-root transformed. We selected the first four PCA factors collectively accounting for 79 % of environmental variability between plots. Factor 1 was primarily linked to the structure of the ground habitat (% ground cover of bare ground, stones and rocks, and the complexity of the ground habitat), factor 2 was primarily linked to the vertical profile of the vegetation (% cover of trees and shrubs), and factors 3 and 4 were primarily linked to aspect (and to some extent to altitude) and to plant species richness respectively (Mandelik et al. 2012). We converted the PCA factors into Euclidean distances and calculated a habitat similarity matrix representing the similarity in habitat structure between pairs of plots. Using a Mantel test, we correlated the habitat similarity matrix with a matrix containing a score of "0" for pairs of road edge plots and pairs of control plots, and a score of "1" for pairs of road edge + control plots (ANOVA-like

Mantel; Sokal et al. 1993). No significant correlation was found between the two matrices (9,999 randomizations;  $Z = 633$ ;  $p = 0.1$ ), indicating no significant difference in habitat structure between the road edge and the control plots.

### Statistical analyses

We analyzed differences between the road edge and the control plots in species richness, abundance, rarity (proportion of rare species out of total number of species), endemism (proportion of endemic species out of total number of species), and disturbance-associated plants (proportion of disturbance-associated plant species out of total number of plant species) using  $t$  and Mann–Whitney tests, depending on normality and homogeneity of variances of transformed variables. To further explore possible larger distance effects of the road we regressed richness and abundance data of the control plots against their respective distance from the road; for richness and abundance data of the species rich taxa as well as abundance data of the species poor taxa we used linear regression, and for the species richness data of the species poor taxa we used Spearman correlation. To achieve normality and homogeneity of variances abundance and richness variables were square-root transformed and the proportion of rare, endemic and disturbance-associated species were arcsine transformed. To explore differences between the road edge and control plots in cumulative richness and abundance-standardized richness, we constructed cumulative species richness curves using the analytic Mao Tao richness estimator (Colwell et al. 2004; EstimateS version 8.2, <http://viceroy.ceb.uconn.edu/estimates>; Colwell 2009) for the species-rich taxa. For the species-poor taxa, the effect of abundance on estimates of species richness is expected to be limited and was thus not explored.

We analyzed differences between the road edge and the control plots in species composition using Mantel tests on a species similarity matrix and a habitat matrix containing a “0” score for pairs of road edge plots and pairs of control plots, and a score of “1” for pairs of road edge + control plots. We visualized the results of the Mantel tests using non-metric multidimensional scaling (NMDS; PC-ORD version 5, MjM Software, Gleneden Beach, Oregon). NMDS is used to find and graphically display the configuration of an ordination space in which distances between samples best represent pairwise dissimilarities in species composition in a reduced number of dimensions (Clarke 1993; Leps and Smilauer 2003). For both the Mantel and the NMDS, we used the relative Sorensen measure to account for variability in overall and species-specific abundances.

We analyzed the trophic composition of the beetle community (relative species distribution among the different trophic guilds) in the road edge versus the control plots using likelihood-ratio G tests. We estimated the average cumulative number of species in 10 out of 12 control plots using 1,000 bootstrap simulations.

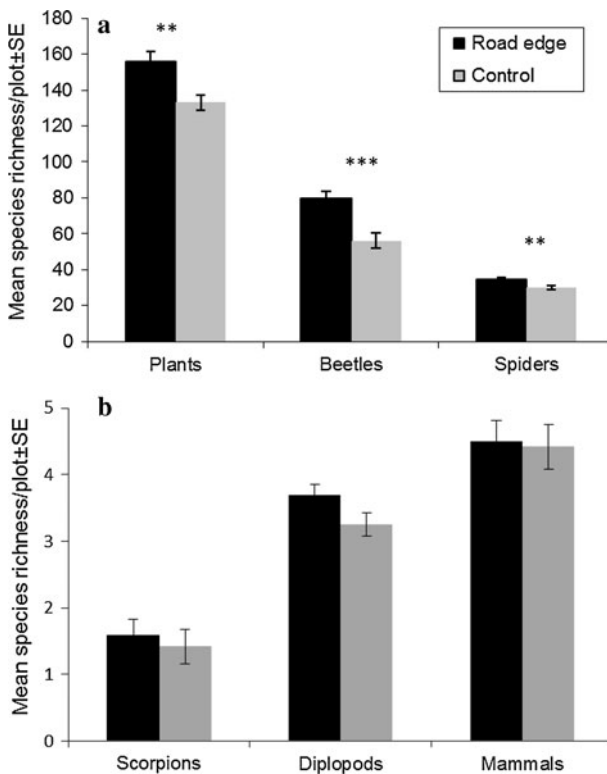
## Results

We sampled a total of 333 plant species, 5,027 beetles belonging to 211 species, 4,576 spiders belonging to 84 species, 103 scorpions belonging to 5 species, 773 diplopods belonging to 4 species, and 356 mammals belonging to 8 species.

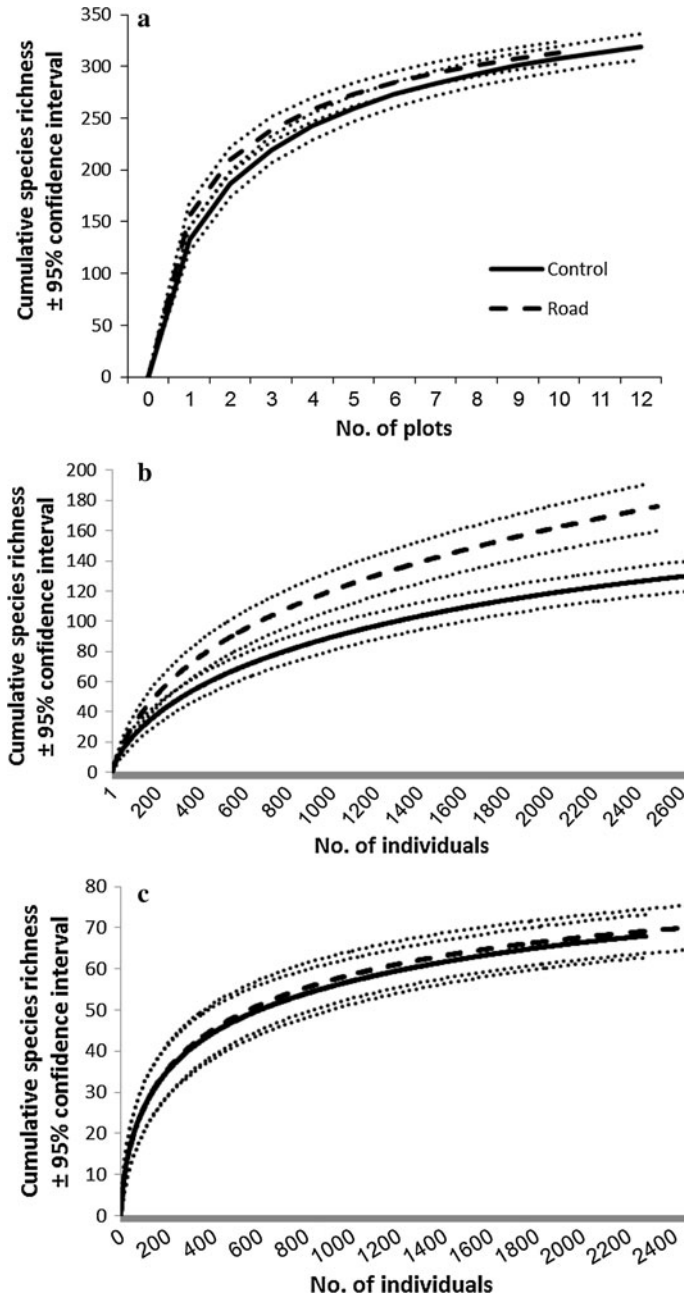
Mean species richness of plants, beetles, and spiders was significantly higher in the road edge compared to the control plots (plants:  $t_{20} = -3.22$ ,  $p = 0.004$ ; beetles:  $t_{20} = -3.94$ ,  $p < 0.001$ ; spiders:  $t_{20} = 3$ ,  $p = 0.007$ ) (Fig. 1a); in the species-poor taxa, we found no significant differences in mean species richness between the road edge and the control plots

(scorpions:  $Z = 0.36$ ,  $p = 0.72$ ; diplopods:  $Z = 1.55$ ,  $p = 0.12$ ; mammals:  $Z = -0.03$ ,  $p = 0.97$ ) (Fig. 1b). Mean abundance of spiders, scorpions, and mammals was significantly higher in the road edge compared to the control plots (spiders:  $t_{20} = -3$ ,  $p = 0.007$ ; scorpions:  $t_{20} = -2.77$ ,  $p = 0.012$ ; mammals:  $t_{20} = 3.58$ ,  $p = 0.002$ ), while beetle abundance did not differ significantly between the two plot types ( $t_{20} = 1.18$ ,  $p = 0.25$ ), and diplopod abundance showed the opposite trend and was significantly higher at the control plots ( $t_{20} = -3.44$ ,  $p = 0.002$ ). When exploring larger distance effects of the road, we additionally found significant negative relations between distances of the control plots from the road to species richness of plants (Beta =  $-0.624$ ,  $F_{(1,10)} = 6.384$ ,  $p = 0.03$ ), and to abundances of spiders, scorpions and mammals (spiders: Beta =  $-0.756$ ,  $F_{(1,10)} = 13.31$ ,  $p = 0.004$ ; scorpions: Beta =  $-0.708$ ,  $F_{(1,10)} = 10.07$ ,  $p = 0.01$ ; mammals: Beta =  $-0.83$ ,  $F_{(1,10)} = 22.15$ ,  $p = 0.001$ ). No significant relations were found between distances of the control plots to the road and richness and abundance measures of the other taxa. The accumulated beetle species richness was higher in the road edge plots compared to the control throughout the measured abundance range, while the two accumulation curves for the plants and the spiders largely overlapped (Fig 2).

The proportion of rare and endemic plant and beetle species was significantly higher in the control than in the road edge plots (rarity: plants  $t_{20} = 2.614$ ,  $p = 0.017$ ; beetles  $t_{20} = 3.493$ ,  $p = 0.002$ ; endemism: plants  $t_{20} = -2.7$ ,  $p = 0.013$ ; beetles  $t_{20} = -3.1$ ,  $p = 0.006$ ), while the proportion of disturbance-associated plant species was significantly



**Fig. 1** Mean species richness of **a** species-rich taxa (plants, beetles and spiders), and **b** species-poor taxa (scorpions, diplopods and mammals), in road edge versus control plots. \*\* $p < 0.01$ ; \*\*\* $p < 0.001$



**Fig. 2** Species accumulation curves in the road edge versus control plots for **a** plants, **b** beetles, and **c** spiders

higher in the road edge compared to the control plots ( $t_{20} = -11.16, p < 0.001$ ). We found no significant difference in spider rarity between the road edge and the control plots ( $t_{20} = 0.163, p = 0.87$ ).



Species composition of the species-rich taxa was significantly affected by proximity to the road edge, though it accounted for only 18–24 % of the variation in these communities (Table 1). Accordingly, the NMDS of the species-rich taxa showed clear separation of the road edge versus the control communities (Fig. 3). The road edge had no significant effect on the scorpion and mammal species composition (Table 1). Diplopod species composition was significantly affected by the road edge, but it accounted for only 10 % of the variation in this community. No reliable NMDS was found for the species-poor taxa (Stress factor >35; Table 1).

We found no significant differences between the road edge and the control plots in overall trophic structure of the beetle community, i.e. relative abundance of herbivores, predators, and decomposers ( $G = 0.59$ ,  $df = 2$ ,  $p = 0.74$ ). However, the decomposer guild contained a significantly larger proportion of species foraging on animal matter than on plant matter in the road edge compared to the control plots (the decomposer guild contained 34 versus 16.6 % of species foraging on animal matter in the road compared to the control plots respectively;  $G = 4.42$ ,  $df = 1$ ,  $p = 0.036$ ).

## Discussion

All of the road edge communities we studied showed significant differences in one or more of the community parameters explored, i.e. species richness, abundance, and composition, compared to the control communities sampled a few hundred meters away. However, we found no corresponding differences in habitat structure between the road edge and the control plots, based on the measures we used. Hence, the effects of the road edge on adjacent communities apparently resulted from changes in environmental conditions other than habitat structure that affected habitat associations and/or individual survival. The diverse taxonomy, phylogeny, and trophic levels of the taxa we studied, enhance the applicability of our conclusions to other small-bodied ground dwelling taxa.

Increased species richness in disturbed habitats is a phenomenon well known from a variety of systems and taxa (e.g. Petraitis et al. 1989; Angold 1997; McCabe and Gotelli 2000). One explanation for this phenomenon is presented by the intermediate disturbance hypothesis (Connell 1978), according to which natural or anthropogenic disturbances of

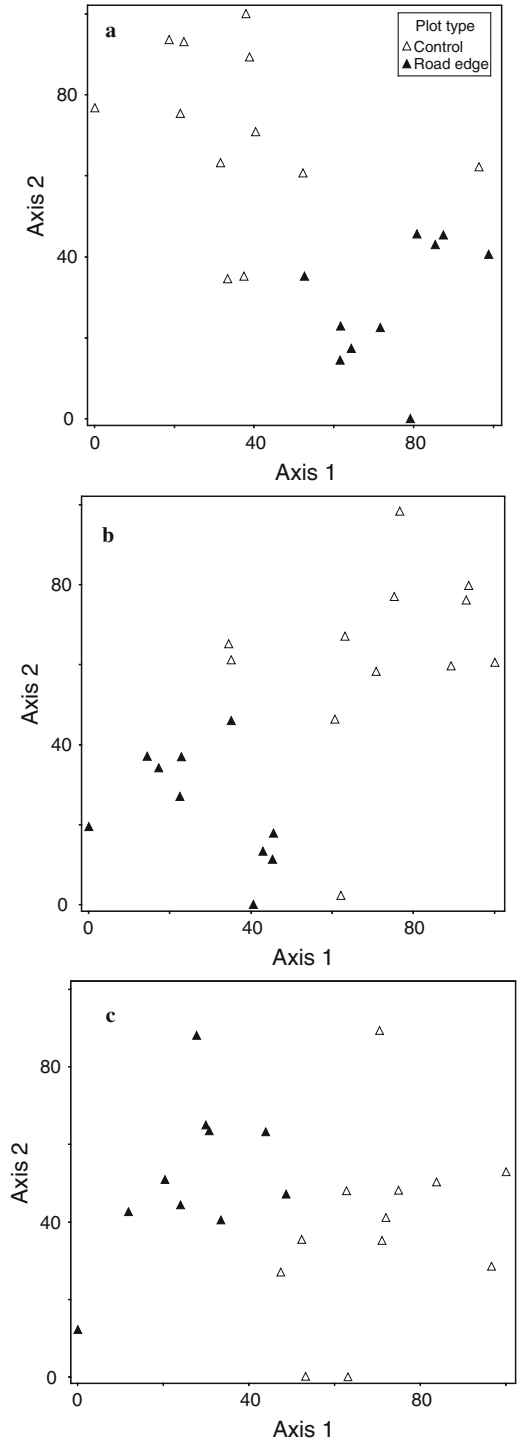
**Table 1** Results of the mantel tests and non-metric multidimensional scaling (NMDS) for exploring differences in species composition between the road edge and the control plots

Taxon	Mantel $r^2$	Mantel Z	Mantel $p$	NMDS number of dimensions selected	NMDS stress <sup>a</sup>	NMDS instability <sup>b</sup>
Plants	0.24	117.3	<0.001	3	8.53	0.00019
Beetles	0.18	134.5	<0.001	2	16.16	<0.00001
Spiders	0.19	102.1	<0.001	3	9.144	<0.00001
Scorpions	<0.01	84.96	0.43	No reliable NMDS was found	>35	
Diplopods	0.1	88.44	0.003	No reliable NMDS was found	>35	
Mammals	<0.01	84.14	0.53	No reliable NMDS was found	>35	

<sup>a</sup> Stress is the overall fit of the ordination, which is inversely related to the match between the dissimilarity indices and the distance in the ordination between pairs of sites (McCune and Grace 2002)

<sup>b</sup> Instability is the variation in the stress measure between subsequent runs of the ordination algorithm; low instability values of around  $10^{-4}$  indicate higher confidence in the stress measure

**Fig. 3** Non-metric multidimensional scaling (NMDS) ordination using the relative Sorensen similarity measure of **a** plant species, **b** beetle species, and **c** spider species



medium intensity, duration and frequency reduce the dominance of local species, and allow niche colonization by other species in the system; this is manifested by a rise in total species richness, and at times by compositional changes (Rosenzweig 1995). The additional species, including exotic ones, often display high rates of reproduction and growth (Wein et al. 1992; Pauchard and Alaback 2004). The increase in floral species richness in the road edge habitat was associated with an increased proportion of disturbance-associated species, while the proportion of rare and endemic species significantly decreased at the road edge compared to the control. Roadside vegetation is generally of poor physiological condition (Moritz and Breitenstein 1985), expressed as low growth rates, sensitivity to pathogens (Northover 1987; Angold 1997) and low survival of seedlings (Fleck et al. 1988). All these weaken the competitive ability of local species while enabling the proliferation of new, disturbance-associated species having higher resistance and growth rates in a disturbed habitat.

The increased species richness of the beetle and spider communities along the road edge compared to the nearby natural area may be caused directly by changes in abiotic conditions such as soil properties, microclimatic conditions and the high concentration of pollutants. All of these may enable the establishment of disturbance-tolerant opportunists (Gobbi and Fontaneto 2008), or some stenotopic species (Eversham and Telfer 1994). Road edges, because of their flattened ground which provides relative ease of movement, may also be a preferred dispersal corridor for ground dwelling beetles and spiders (Koivula 2005). An additional, not mutually exclusive, explanatory mechanism is the indirect effect of higher plant species richness which directly or indirectly increases the variety of foraging resources available to these taxa along the road edge. The correlations found between floral richness and beetle and spider richness (Mandelik et al. 2012) strengthen this argument. Indirect plant-mediated effects of the road on animal groups can also explain the extended effects of the road recorded among the control plots located 550 and up to 1,700 m from the road, as direct road edge effects are restricted to smaller distances (Forman and Alexander 1998).

The effect of the road edge on plant and spider species richness was limited to the plot level (mean richness per plot) while their overall accumulated species richness and the rate of species accumulation did not differ between the road edge and the control. In the beetle community, on the other hand, plot level richness, overall accumulated richness and species accumulation rate were all higher at the road edge. Hence, at the community level, the main effect of the road edge on plants and spiders is probably compositional, i.e. changes in species identities but not in their overall number, while for the beetle community, the road edge affects both the identity of species and their overall number; this is similar to findings in other studies (Koivula 2005; Melis et al. 2010).

Despite the clear distinction between plant, beetle and spider species composition in the road edge versus the control plots, as seen in the ordination diagrams, the road edge/control classification of plots had limited explanatory power. In addition, the heterogeneity of the natural plots themselves accounts for a similar proportion of variation in species composition as the classification of road edge/control (<20 %) (see Mandelik et al. 2012). Hence, though the road does affect the composition of these taxa, other factors, possibly related to micro-habitat conditions and species specific requirements may have overriding influences.

The road edge affected not only the overall composition of the beetle community, but also its trophic structure, and possibly its decomposition activity as well (though no direct data on decomposition function was collected in this study). The increase in the proportion of decomposer species living on animal matter in the road edge habitat may be attributed to higher density of food sources such as road kill and dung in the road edge plots. Similar

positive effects of roads have been found for other carrion consumers such as vultures (Coleman and Fraser 1989). The area surrounding roads may be characterized by increased activity of animals, which are either attracted to roads as a preferred foraging or nesting site (Cowardin et al. 1985; Coleman and Fraser 1989), or abstain from crossing them, usually moving alongside them (Merriam et al. 1989; Baur and Baur 1990; Koivula and Vermeulen 2005). All these increase the likelihood that excrement will be present. Sporadic field observations have shown a higher incidence of carcasses on the road surface and its margins, relative to the control plots.

The ecologically significant effects of the road edge on species-poor taxa were confined to their abundance parameters. In these taxa, the lack of road edge effect on species richness and composition might be connected to the low number of species, which limits detection of any species level effects, or to limited sensitivity of these populations to road edge conditions. The decreased abundance of diplopods near the road might be linked to adverse habitat conditions found along the road edge such as decreased soil moisture and increases in compaction, temperature, and concentration of heavy metals (Trombulak and Frissell 2000). Similar negative effects of roads on soil fauna have been found in other studies (Guntner and Wilke 1983; Haskell 2000). The increased abundance of scorpions and small mammals along the road edge may be due to the increased availability of foraging resources through the rise in abundance and/or richness of the species-rich taxa. Reduced risk of predation along the road resulting from negative road edge effects on predators of scorpions and small mammals (Fahrig and Rytwinski 2009) may also contribute to this phenomenon. Similar positive effects of roads on rodents have been found in other studies (Adams and Geis 1983; Gerland and Bradley 1984; Rytwinski and Fahrig 2007; McGregor et al. 2008; Bissonette and Rosa 2009), pointing to a general positive association between rodent abundance and roads (Fahrig and Rytwinski 2009).

## Conclusions

In summary, we found a variety of community level effects of the road edge on the structure, composition, and possibly the function of the studied communities. The extent of these effects varied among taxa, but they were generally positive or neutral, and evident mostly for the species-rich taxa. A plausible explanation for the generally positive effect of the road edge is the relatively small habitat ranges coupled with high reproductive rates of the studied taxa, which enable them to persist in the area bounded by roads while suffering low mortality (Fahrig and Rytwinski 2009). While we observed increased richness and abundance along the road edge that extended hundreds of meters into the surrounding landscape, the contribution of the road edge habitat to biodiversity conservation in the region may be limited, as revealed by the altered species composition and decreased proportion of species of high priority for conservation in the road edge communities. However, mapping community level patterns is only the first step toward better managing and mitigating road edge effects (Roedenbeck et al. 2007). To gain a wider perspective on long-term processes shaping road edge communities, it is important to explore survival and fitness of individuals and viability of populations inhabiting the road edge habitat. In some cases, road edges were associated with increased rates of predation, parasitism, and offspring mortality (Batáry and Báldi 2004; Ries et al. 2004), indicating that road edges may act as ecological traps (Ries and Fagan 2003) and have an overall negative effect on the conservation of plants and small animals in the area. As we have shown, community level effects of the road can extend hundreds of meters from the road, and cover large areas.

Thus, a thorough understanding of both patterns and processes shaping road edge communities is required to fully evaluate the ecological effects of roads and the mitigation of those effects. Finally the species-rich taxa, including plants, ground-dwelling beetles, and spiders, exhibited a variety of community level changes related to the altered habitat conditions along the road edge, and could thus be used as indicators for community level changes in monitoring programs for this ecosystem.

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