Journal of Natural History, 2013
http://dx.doi.org/10.1080/00222933.2012.743610

Road edge effects on litter invertebrate communities of subtropical forests

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(*Received 28 October 2011; final version received 21 October 2012*)

We assessed road edge effects on leaf-litter macroinvertebrates in laurel and pine forests in Tenerife (Canary Islands), studying composition, abundance, richness and diversity, and the role of environmental gradients. We sorted species to the finest taxonomic resolution possible and used a morphospecies approach when necessary. In all, 15,824 invertebrates were identified from 388 litter samples (from >500 species, five major phyla and 31 orders). Alien invasive species of Oligochaeta, Pulmonata, Isopoda, Diplopoda and Hymenoptera were frequent in both forests. Richness, diversity and rarefaction pointed to a disturbance threshold within the first 10 m off the road, and edge effects were steeper in laurel forest than in pine forest. Overabundant aliens were partially responsible for highly disturbed litter assemblages on this edge zone in both forests. Proximity to road edge caused gradients of disturbance of forest structure. Litter moisture, rock and litter cover in laurel forest, and grass and canopy cover in pine forest were the best predictors of community variation. Results seemed to give some empirical support to the intermediate disturbance hypothesis. This altered road edge zone may accumulate regionally causing net reductions of ecosystem area and quality, impacting on its integrity and biodiversity.

Keywords: arthropods; non-arthropod invertebrates; laurisilva; *Pinus canariensis*; rarefaction

Introduction

As ecological boundaries, road edges play numerous roles, acting as complex, dynamic entities that vary in space and time, and are strongly dependent on the traversed ecosystem and its particular disturbance processes (Milne et al. 1996; Schlaepfer and Gavin 2001). Along and across forest-road edges, the rate of change in structure, dynamics and species richness and composition are often high and different from the core ecosystem, as occurs at frontiers between forest and non-forest areas (Yahner 1988, Fortin 1994). Road edges are therefore conceived as marginal zones with a distinctive composition and abundance of organisms (Forman 1998), where the traditional concept of ecotone is applicable (Risser 1995).

Both negative and positive impacts of roads on the biota, expressed as responses of organisms in terms of composition, abundance or diversity, are perceived along and across their edges (Trombulak and Frissell 2000; Forman and Deblinger 2000; Hansen

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*Corresponding author. Email: jddelgar@upo.es and Clevenger 2005). Road division of ecosystems induces edge effects, connectivity changes and area reduction (see reviews in Bennett 1991; Forman and Alexander 1998; Spellerberg 1998). Roads also promote structural and functional alterations that penetrate the traversed landscape matrix reaching variable distances (Forman et al. 2002). Different road edge effects, or effects on distinct components of the biota and the environment, may be spatially delineated to assess the extent of changes in the affected ecosystems. Hence, the understanding of road edge effects transcends their importance for local communities to have a resonance at the entire landscape level (Sarlöv 2001; Forman et al. 2002).

Very little is known about road edge effects on inconspicuous, but ecologically critical components of the biota (e.g. bacteria, protozoa, fungi, lichens, mosses, soil invertebrates, parasites, most alien species) so it would be helpful to establish a multifactorial delineation of edge effects. In the invertebrates, the majority of studies are devoted to conspicuous or large arthropod species or to taxonomically limited groups, upon which mostly idiosyncratic responses have been found (e.g. earthworms, snails, spiders, ticks, centipedes, millipedes, butterflies, carabid beetles, bees, ants) (McEnroe 1971; Ash and Lee 1980; Baur and Baur 1990; Mader et al. 1990; Gonseth 1992; Kubach and Zebitz 1996; Samways et al. 1996; Bhattacharya et al. 2003; Keller and Largiader 2003; Kalisz and Powell 2003).

Disturbances to the soil fauna have consequences for higher trophic levels and larger organisms that rely on them, such as other invertebrates, higher plants and birds (Didham et al. 1996; Hilty and Merenlender 2000). Despite their influence at multiple scales, the role of road edge effects on the forest matrix and on ground invertebrate communities remains poorly known. Road schemes, the environmental impact assessment process, biodiversity assessments of projects, and roadside management would greatly benefit from the analysis of road influences and the modelling of biotic–environmental interactions caused by roads for fine-grained, discretely distributed biological indicators, such as ground invertebrates.

Here we explore how forest roads affect biodiversity and community structure of a whole assemblage of litter invertebrates on an oceanic island. We focused on road edge effects of paved and unpaved roads in two subtropical forests of the Canary Islands, the evergreen laurel forest and the Canarian pine (*Pinus canariensis*) forest. In these ecosystems, roads create steep disturbance gradients that have been described with respect to microclimate, vegetation and vertebrate fauna along the road–forest interior gradient (Delgado et al. 2001a,b, 2008; Delgado et al. 2007a; Delgado et al. 2007b; Arévalo et al. 2008, 2010). Here we analyse changes in: (1) invertebrate species composition, relative population density or abundance, species richness and diversity; (2) variation in environmental factors (vegetation and litter structure) with road proximity, and their relationships with the invertebrate community. We also compared these edge-to-interior patterns in litter fauna and microhabitat between two contrasting corridor types (asphalt roads and unpaved dust trails) and topographic locations of transects.

Study areas

Field work was carried out in laurel (“laurisilva”, an evergreen cloud forest) and Canarian pine forests in Tenerife (3718 m elevation, 2036 km^2), in the Canarian

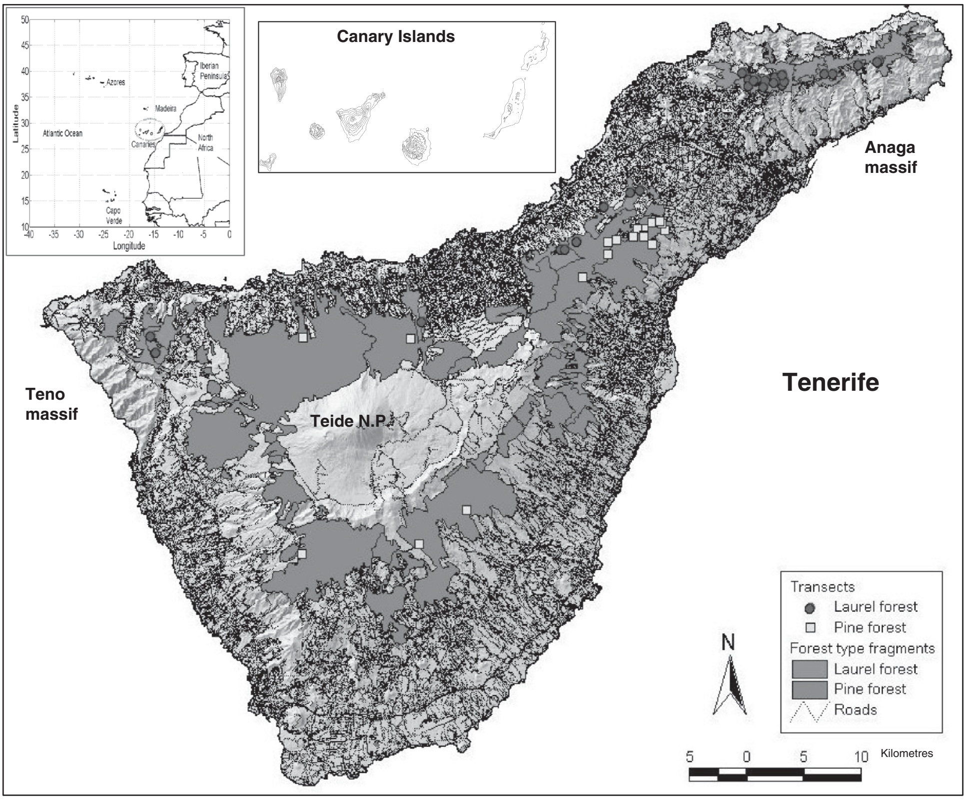

Figure 1. Location of study transects on the two main forest ecosystems on Tenerife, Canary Islands.

Archipelago (28°19' N, 16°34' W) (Figure 1). They form altitudinal belts at 600–1100 m on the windward slopes (laurel forest), and 800–2000 m on both windward and leeward slopes (Canarian pine forest). The laurel forest occupies 4027 ha in Tenerife (10% of the potential area) and the pine forest occupies 36,740 ha (80% of the potential area). All study sites were located between 700 and 1090 m and between 1025 and 1690 m above sea level in laurel and pine forests, respectively (Appendix 1). Average slope at the study sites was 15° in laurel forest and 13.5° in pine forest. The study encompasses the major remnants of laurel forest (Teno and Anaga mountains) and pine forest (Corona Forestal Natural Park).

The laurel forest canopy (up to 10–20 m height) and upper understorey (3–5 m) is dominated by *Laurus novocanariensis*, *Myrica faya*, *Ilex canariensis*, *Erica arborea*, *Prunus lusitanica*, *Viburnum tinus* and *Erica scoparia* on exposed ridges. Other locally frequent trees in laurel forest are *Apollonias barbujana*, *Heberdenia excelsa*, *Persea indica* and *Picconia excelsa*. The pine forest canopy (20–30 m height) is formed by *Pinus canariensis*, and *M. faya*, *E. arborea*, *Chamaecytisus proliferus*, *Adenocarpus viscosus*, *Daphne gnidium* and *Cistus symphytifolius* are present in the understorey.

Methods

Transect selection and construction

We selected a broad range of forest situations with respect to roads at the island scale. So, we made an effort to limit sources of habitat variation affecting litter communities. We searched for sites fulfilling these requirements: (1) avoidance of recent human disturbances such as removal of wood, foliage or litter; (2) transects did not overlap with other linear elements like fire breaks, power lines, marginal habitation areas or agricultural land; (3) minimizing the effects of strong reliefs (abrupt ravines, steep road embankments) (Miller et al. 1996). All transects, excepting two that were 75 m apart, were at least 100 m apart in an attempt to study different edges and to minimize spatial autocorrelation and pseudoreplication at the landscape scale (Honnay et al. 2002).

Corridor types were paved roads and unpaved roads (dust trails). We constructed 31 transects in laurel forest (18 in paved roads, 13 in dust trails) and 20 in pine forest (11 roads, 9 trails). All road segments were relatively narrow: 7.2 ± 1.4 m (mean ± 1 SD) and 5.2 ± 2.2 m for laurel forest asphalt roads and dust trails, and 8.4 ± 1.9 m and 6.6 ± 1.7 m for pine forest roads and trails, respectively (Appendix 1).

In both forests, transects ran at right angles from the edge of the road right-of-way to the forest interior (Figure 2). On these transects, leaf litter was sampled at the following distances from roads: 1, 3, 6, 10, 20, 40, 60 and 100 m (Figure 2). Our initial intention was to construct all transects extending 100 m into the forest, but there were some landscape constraints. In laurel forest, the high density of roads, trails, footpaths, recreation and cleared or agricultural areas hampered construction of 100-m-length transects in every site. As a result, the length of several transects in laurel forest was <100 m to avoid major overlaps and the total length of laurel forest transects was as follows: 20 m ($n = 1$), 40 m ($n = 5$), 60 m ($n = 6$), 100 m ($n = 19$). The total area

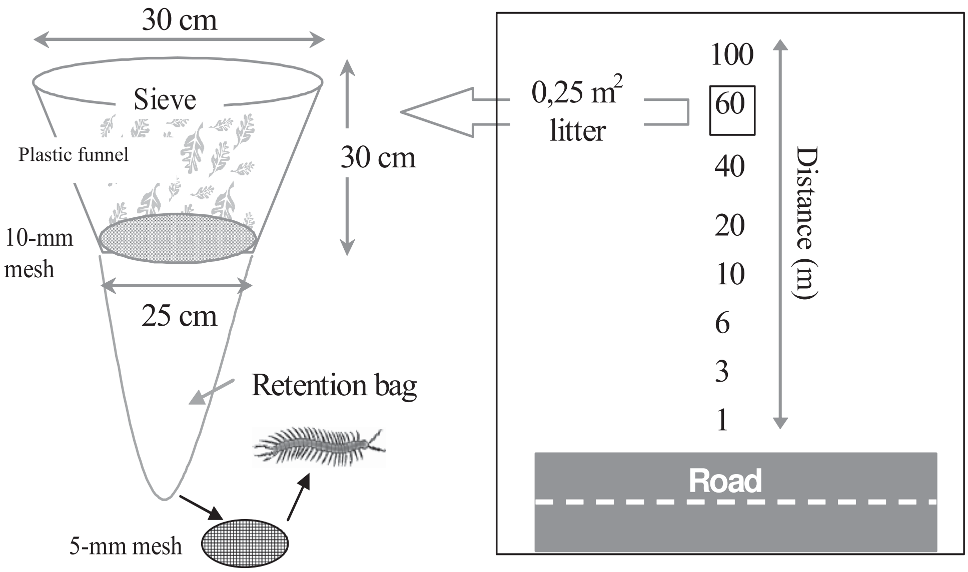

Figure 2. Scheme for litter invertebrate sampling along road–interior gradients.

available to locate transects that did not overlap with other infrastructures was larger in pine than in laurel forest, so all 20 pine forest transects were 100 m in length.

The distance intervals were chosen following the expectations that: (1) a higher rate of change of litter communities is to be found near edges (Didham et al. 1998; Haskell 2000); and (2) main environmental and vegetation gradients occur in the first few meters of the laurel and pine forests for these narrow roads (Delgado et al. 2007b; Arévalo et al. 2008). Many environmental edge effects (excluding wind) potentially affecting invertebrate distributions, are commonly recorded within 100 m of edges in other regions (Laurance 1991; Forman et al. 2002). Hence, our 100-m transects were a trade-off between trends to overestimate or underestimate (fail to find a net pattern) edge effects (Laurance 1991). Transects were distributed fairly equally between above-road and below-road positions to evaluate the effects of slope on litter communities.

Litter sampling

Leaf litter was sampled for invertebrates during 2000–01 and 2001–02. Sampling took place diurnally on dry days, in the absence of rain or strong wind. This would minimize the falling of canopy invertebrates (chiefly arthropods) to the ground litter compartment, which would introduce another big source of bias in our litter community characterization. Each individual transect was sampled entirely within 1.5–2.5 hours. The leaf litter was formed by evergreen lauroid and ericoid leaves (mostly from dominant species, especially *Laurus novocanariensis* and other lauraceae, with *Myrica faya*, *Ilex canariensis* and *Erica arborea*) in laurel forest, and almost exclusively by needles in *Pinus canariensis* forest. On each transect, leaf litter was rapidly scraped by hand from one 50 × 50-cm square (area = 0.25 m^2) placed at each sampled distance from the road edge. Litter was placed in a labelled plastic zipper-top bag and transported to the laboratory for processing. In the laboratory, litter bags were placed in a cool half-light area until analysis. In total, 93.4 kg of litter ($n = 228$ litter bags) was collected in laurel forest (mean ± SD, Standard Deviation per distance = 395.9 ± 214 g) and 49.2 kg ($n = 160$ litter bags) in pine forest (307.6 ± 199.3 g).

Extraction of the litter fauna

To extract the fauna, litter samples were vigorously shaken for 1–2 minutes through a 10-mm wire mesh (Figure 2). This allowed us to retain the larger faunal specimens ($\geq$1 cm, e.g. large slugs and snails) and to sort out the friable litter and pebble/stone fractions, which were examined for adhered specimens. The resulting finer fraction was collected in a bag attached to the sieve and passed through a new 5-mm mesh on a clear-coloured dissecting dish (40 × 30 × 2 cm). All mesoinvertebrates and macroinvertebrates ($\geq$2 mm length or diameter) were picked by hand from the dish with fine surgery forceps or with a wet hair brush and transferred, by major taxa, to separate vials of appropriate size. Preservation of specimens was made with 70% ethanol, except for beetles, which were preserved in Scheerpeltz liquid (70% ethanol/acetic acid/water in a ratio of 65/10/25%) (Southwood 1978).

By this manual protocol, we could process each litter sample in between 30 minutes and 3 hours, whereas much more time (days or weeks) is required by other standard methods. We used this procedure after preliminary trials with pilot samples using other techniques such the Berlese funnel. Such techniques are very useful for certain groups but extract different taxa with very different efficiencies (Southwood 1978), and we were interested in sampling, as thoroughly as possible, and with a comparable sampling efficiency, the litter species pool from a large number of samples.

Identifying the litter fauna

A critical step when interpreting road disturbance effects is to know as completely as possible the taxonomical spectra under analysis. With soil invertebrates this is a complex task because of the inherent high species number (Giller 1996), the difficulty of taxon sorting, and the labour-intensiveness of identification and classification. Comprehensive natural history information on the litter invertebrate fauna of the Canarian forests is scattered in the specialized, mostly taxonomical literature. Hence, a goal of this study was, first, to describe the species composition of the leaf litter compartment.

To identify species, published keys on Canarian and related fauna were used for the best-known groups. When necessary, specimens were identified with the aid of a stereomicroscope under a 10 × magnification. Once identified, we retained reference specimens for further comparisons. Specimens that we could not readily identify were placed in vials, sorted by major taxa (from genera to phyla), labelled and stored until detailed identification or submission to specialists (listed in Acknowledgments).

In many instances, it was not possible to achieve the full taxonomic identity of the species. We then referred to the closest higher taxa or morphospecies (Hammond 1994). Krell (2004) proposed the use of the term parataxonomic units when sorting samples to recognizable taxonomic units. This is a useful (though not necessarily conservative) strategy to estimate α-diversity (specific richness) and β-diversity (compositional change), because the actual species number and the number estimated as morphospecies are significantly correlated (Oliver and Beattie 1996; Krell 2004).

Our main source of overestimation of species number comes from infra-order levels (i.e. genera), especially those with many immature individuals or sexes of groups with marked sexual dimorphism (i.e. theridiid and linyphiid spiders). For example, in many spiders, sorting to different morphospecies is risky because juvenile individuals display great variation in abdominal patterns and females are commonly different from males (Roberts 1995). Hence, in case of absence of both adults, we grouped all immature and female individuals within a family, and, when possible, genus, subsequently including individuals with similar abdominal patterns into the same morphospecies.

The pre-imaginal stages of insects (larvae, pupae and chrysalides) were sorted to order, family, genus, morphospecies, or actual species whenever possible (namely, in cases where there was no confusion, i.e. when only the larvae appeared, e.g. *Myrmeleon alternans*). By including these stages in the counts, we could be inflating the number of morphospecies present. However, we considered this source of bias to be negligible, because the intraspecific niche division in these insects allows larvae and adults to exploit very different spatio-temporal niches. Hence, functional and taxonomical diversity were, probably, not importantly overestimated (Giller 1996). Moreover, the vast majority of unidentified species in pre-adult stages were Lepidoptera and Diptera, groups with relatively low representation as flying adults in our passive (i.e. not actively baited) litter samples (Becerra et al. 1992; Báez 1998).

Nomenclature followed Izquierdo et al. (2001), excepting Coleoptera, for which we followed Machado and Oromí (2000).

Habitat variables

At each road–interior transect, we measured road width (WIDTH) and estimated percentage canopy cover above the road centre (CANO) with a convex spherical densiometer (Lemmon 1957). At each sampling square from the road surface, the following data on vegetation and ground substrata were taken: (A) percentage canopy cover (COVER), with a forest canopy densiometer (Lemmon 1957); (2) canopy height (HEIGHT, m), averaged from four visual estimates of the same observer with sighting references of known height; (3) percentage cover of woody shrubs >30 cm and <3 m in height (SHRUB); (4) percentage cover of grasses (<30 cm) (GRASS), by visual estimate; (5) the intercepted number of vertical layers of vegetation (LAYERS) above the quadrant centre; (6) the number of tree and treelet species in a 5-m radius circle centred on the sampling square (TREES, variable evaluated only in laurel forest), to give an indication of diversity of species potentially forming the local leaf litter affecting invertebrate community; (7) percentage cover of the litter layer (LITTER); (8) litter depth (DEPTH, cm), with a ruler after removing the litter, averaging four measures from the four square sides; (9) percentage rock cover (ROCK), for rocks >5 cm diameter; (10) decaying wood >5 cm diameter (WOOD); (11) slope of terrain at the local sampling point (SLOPE), in degrees.

Litter fresh weight (± 0.1 g) was measured before sorting the fauna. After faunal extraction, litter was air-dried over blotting paper at room temperature to constant weight to obtain litter dry weight (WEIGHT). Litter moisture (MOIST) was then calculated as a percentage. The larger stones were sorted, weighed and their weight was subtracted from total weight to obtain the actual litter dry weight.

Data analysis

Abundance, richness and diversity descriptors

The relative population density of invertebrates was expressed as individuals per square metre. As community descriptors, richness or species number (S), species diversity with Shannon's index ($H' = -\Sigma\, p_i\, ln[p_i]$) and Shannon's uniformity ($E = H'/logS$) (Magurran 1988; Spellerberg and Fedor 2003) were calculated for each sample with the SHE module in the BIODIVERSITY PROFESSIONAL 3.2 software package (McAleece 1997).

Composite diversity indices such as Shannon's H can be biased when comparing situations with different species composition or variable population densities of species (Gotelli and Colwell 2001). For this reason, a rarefaction method was complementarily used to estimate the specific richness at the different distances to road and on a species-per-individuals basis. Rarefaction averages the expected number of species from a discrete pool of individuals by resampling at random from a larger set of individuals (Gotelli and Colwell 2001). It is an appropriate approach to the comparison of richness from different sites because these varied greatly in invertebrate abundance, and the rarified species richness takes into account both species numbers and abundance.

Also, this method allowed us to know whether the species detected come from a large or from a small species pool in both laurel and pine forests. Rarified species richness was estimated by Monte Carlo simulations in BIODIVERSITY PROFESSIONAL 3.2, with 1000 randomizations.

Contrast of edge effects and interactions

The reach of the road edge effect was estimated for invertebrate abundance, species richness (S) and Shannon's diversity (H') with analysis of variance with a post-hoc Helmert contrast (Fraver 1994; Burke and Nol 1998). The Helmert procedure compares the mean value at the edge with the mean value at each distance from the edge, testing for significant differences until the distance beyond which no significant changes appear. The Bonferroni post hoc contrast was applied to correct the critical p-level for multiple comparisons. To analyse the combined effects and variance explained for distance to road edge, road type (asphalt-paved versus unpaved or dust trails), location of transect regarding terrain profile (above versus below road), and their interactions, on abundance, richness and diversity of litter fauna, we applied a general linear model (analysis of variance). All data from the pine forest and abundance data from the laurel forest had to be $\log(x + 1)$-transformed to fulfil parametric requisites (Zar 1996).

Multivariate relationships and ordinations

The multivariate relationships between community composition and abundance, and habitat descriptors, were assessed with Canonical Correspondence Analysis (CCA) (ter Braak and Prentice 1988). This ordination technique is suited for the study of mostly non-linear relationships that are common between habitat data and complex species pools. We tested for statistical significance, under the null hypothesis of no effect, of the associations between predictor variables and litter fauna using Monte Carlo permutation tests with 500 randomizations, under the full model option in CCA. The abundance data were $\log_{10}(x + 1)$-transformed and a down-weighting factor was applied to cope respectively with the skewed abundance distributions and the effect of rare species. To minimize the effects of very rare species (especially taxa represented by only one or few individuals, or present in few transects), we included in the analyses only those species recorded in at least five transects and with ≥ 21 individuals (abundance $>0.15\%$) in laurel forest ($n = 55$ species) and ≥ 8 individuals in pine forest (abundance $>1.05\%$, $n = 12$ species). CCA was applied to both laurel and pine forest data in separate analyses, with the CANOCO v. 4.5 package (ter Braak and Smilauer 1998).

Results

Invertebrate community composition and general taxonomic patterns

In all, 15,824 invertebrates were collected from 388 litter samples, 15,060 in laurel forest ($n = 228$) and 764 in pine forest ($n = 160$). Mean overall faunal density was far larger in laurel forest (264.4 individuals/m^2 ± 227.2 SD) than in pine forest (19.1 ± 28). In all, five major phyla, Platyhelminthes, Nematoda (only in laurel forest), Mollusca, Annelida and Arthropoda, were represented. Thirty orders were recorded in laurel forest and 21 in pine forest, with 31 orders in all (Appendices 2 and 3).

Overall, 526 species were identified, 383 in the laurel forest and 143 in pine forest. Of these, the number recognized as morphospecies or parataxonomic units was 120 in the laurel forest (22.8% of the species pool) and 42 in the pine forest (41.6%). Many of these were pre-imaginal stages of the Orders Coleoptera, Diptera, Lepidoptera, Neuroptera and Trichoptera, and of undetermined insect groups [536 unidentified pre-imaginal individuals (3.6% of all the individuals) in laurel forest and 44 (5.7%) in pine forest].

There were great differences between forests in abundance distributions of taxa. In the laurel forest only 50 species, summing 13.05% of the species pool and 13,076 collected individuals, represented 94% of the whole community (Figure 3). In the pine forest we had to triple the number of species to reach the same percentage (147 species ~94% of the individuals). A total of 128 species in laurel forest and 139 in pine forest were very rare (one or two individuals). However, rare species contributed very differently to global abundance across all transects depending on forest: ≤0.01% in laurel forest and 21.73% in pine forest. In the laurel forest, major groups by order of abundance were Isopoda, Diplopoda (Orders Polydesmida and Julida), Coleoptera, Oligochaeta, Hemiptera and Gastropoda (Appendices 2 and 3). In the Canarian pine forest, major groups were Diplopoda (Order Julida), Coleoptera, Araneae, Oligochaeta Haplotaxida and Gastropoda.

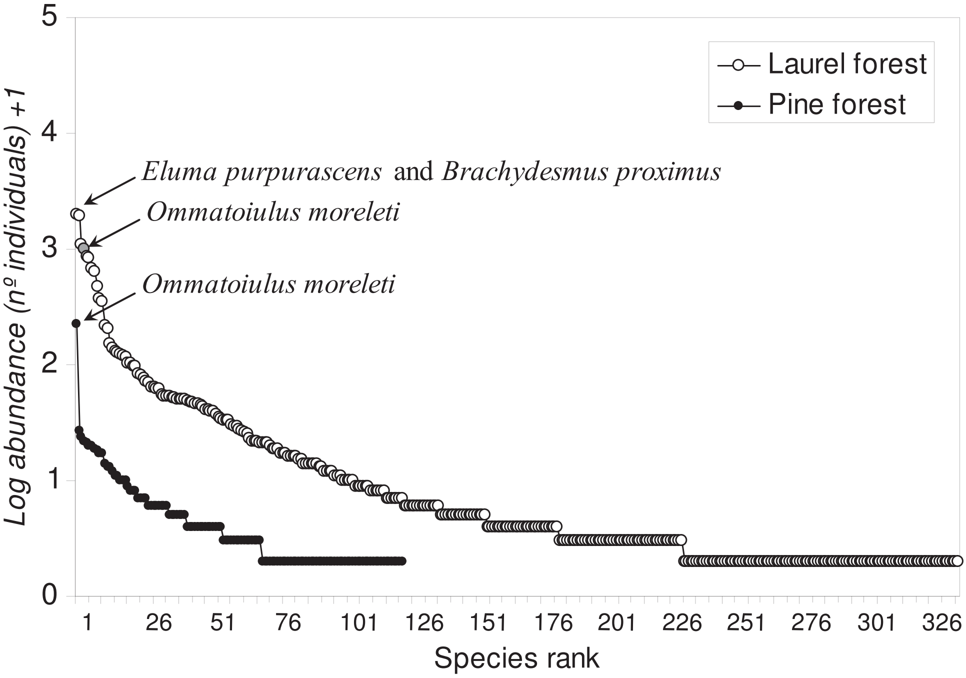

Figure 3. Distribution of logarithmic abundances of litter invertebrate species in laurel and pine forests. Note the position in the rank for most dominant species in each forest (introduced diplopods *Ommatoiulus moreletti* – grey dot in laurel forest – and *Brachydesmus proximus*) and of the isopod *Eluma purpurascens* (arrows).

The single numerically dominant species were *Eluma purpurascens* (Isopoda) (13.1% relative abundance) in laurel forest and *Ommatoiulus moreletti* (Diplopoda: Julida; alien species) (29.6%) in pine forest. In contrast, the two species-rich genera that are characterized by a high adaptive radiation in the Canary Islands, *Dolichoiulus* (Diplopoda: Julida: Julidae) and *Dysdera* (Araneae: Dysderidae), represented only 1.1% of the total litter fauna.

In both laurel and pine forests, 98% of all the recorded species were native to the ecosystem. At least seven exotic species represented 2% of all species in the laurel forest: *Eisenia eiseni* (Oligochaeta: Lumbricidae), *Brachydesmus superus* and *Brachydesmus proximus* (Diplopoda: Polydesmidae), *Brachyiulus pusillus*, *Cylindroiulus truncorum* and *Ommatoiulus moreletti* (Diplopoda: Julidae), and *Hypoponera punctatissima* (Hexapoda: Hymenoptera: Formicidae). The formicid *Plagiolepis schmitzii*, originally described from the southern Palaearctic is not clearly exotic to the Canary Islands (Dr Xavier Espadaler, personal communication). Two of these alien species were also found in pine forest transects (1.6% of all species): *O. moreletti* and *Brachydesmus proximus*. In their work on invasive invertebrates in laurel forest, Arndt and Perner (2008) classified as invasive species the isopods *Eluma purpurascens* and *Armadillidium vulgare*.

Although richness of exotic species was low, their population abundance was exceptionally high in the leaf litter community. The Diplopoda accounted for 22.1% of all the invertebrate individuals collected in laurel forest, and 88.6% of these individuals were from alien species. *Brachydesmus* (two species) and *Ommatoiulus moreletti* were 19.4% of all the litter invertebrates, and *Brachydesmus* spp. alone made up 12.9% of all individuals collected in laurel forest. In the pine forest, *O. moreletti* alone made up 29.6% of the litter fauna collected ($n = 226$ individuals).

In total, 1771 oligochaetes were collected (11.8% of all invertebrate individuals) in laurel forest and 47 (6.2%) in pine forest. The earthworm community in the laurel and pine forest is rich in species, the majority of them exotic (Talavera 1987; Izquierdo et al. 2001). We could not identify all the oligochaetes to species, mainly because of the prevalence of juvenile forms in the litter. The analysis in this group was limited to distinguishing between the families Enchytraeidae and Lumbricidae (Order Haplotaxida). Enchytraeids represented 36% of the oligochaetes in laurel forest and 55.3% in pine forest. The remaining oligochaete species belonged to the Lumbricidae, chiefly to *Eisenia eiseni*.

Road edge effect in abundance

In the laurel forest, overall invertebrate abundance was not affected by a statistically significant edge effect, despite there being a local maximum at 6 m from the edge (Figure 4). For both asphalt and unpaved roads combined, abundance showed a net increase within the first 3–10 m from the edge. However, the net difference in abundance between 1 and 100 m (data from all transects combined) was not significant (Figure 4, Table 1).

Abundance was globally lower in the pine forest than in the laurel forest, and did not differ significantly between edge and interior, despite a local maximum at 10 m from the edge (Figure 4, Table 1).

Road position in the context of sloping terrain interacted significantly with the road edge effect in the laurel forest, but not in pine forest. Abundance in laurel forest

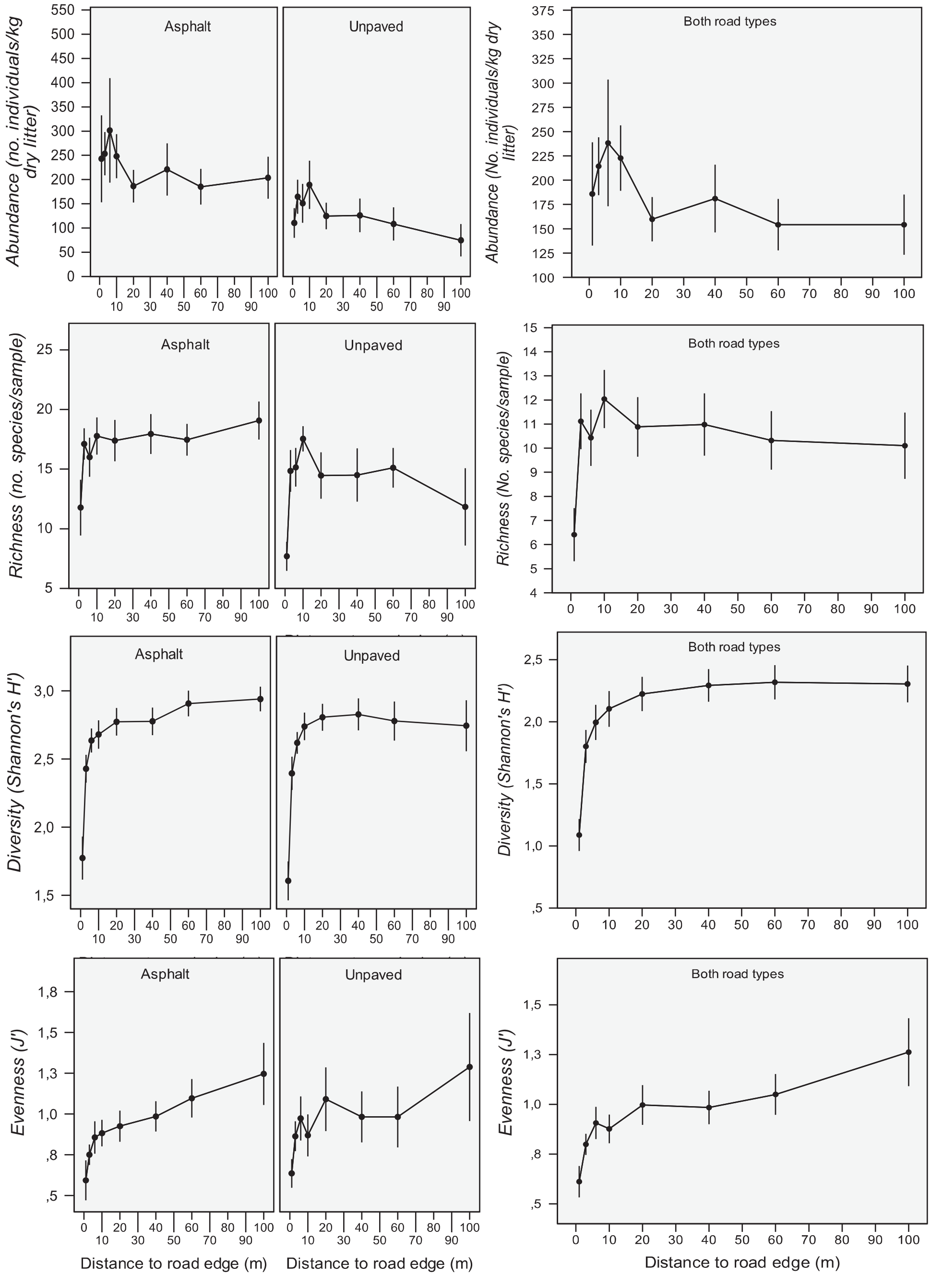

Figure 4. (A) General patterns of richness, diversity and abundance along the road–interior gradient in laurel forest. Mean (dots) ± 1SE (vertical bars) are displayed. (B) General patterns of richness, diversity and abundance along the road–interior gradient in pine forest. Mean (dots) ± 1SE (vertical bars) are displayed.

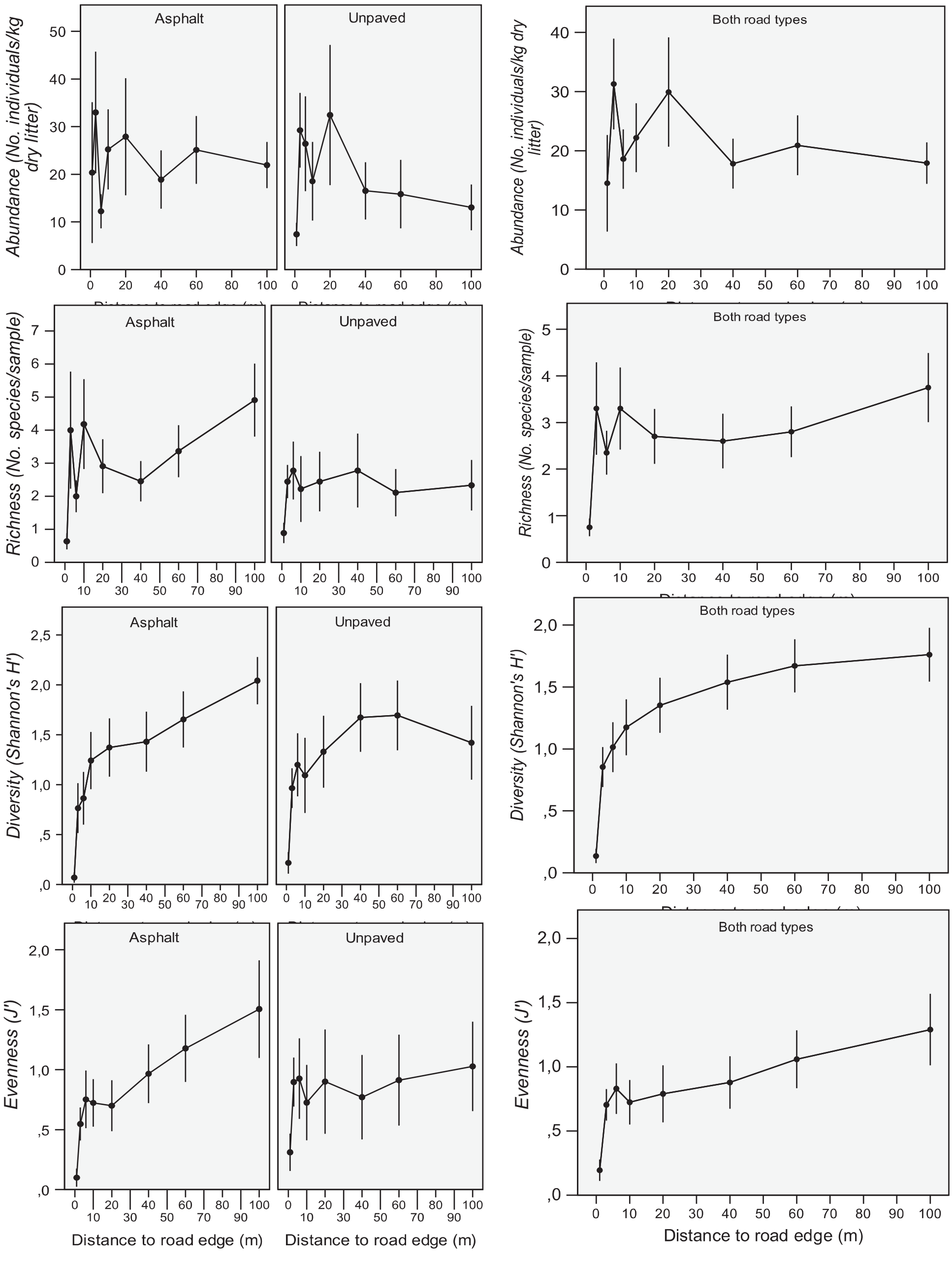

Figure 4. (Continued).

was significantly higher in roadside plots (1–6 m from the edge) below the road (downslope) than in plots above the road (upslope) ($t = 2.76$, $p = 0.006$; Figure 5; Table 2). At further distances, there was no apparent effect of road position regarding terrain profile.

Table 1. Estimates of distance reached by edge effects (unpaved and asphalt roads pooled) on abundance, richness and diversity of litter fauna in laurel and pine forests.

Descriptor	% average net change between gradient extremes	Edge effect reaching distance (m)	F (Helmert contrast)
Laurel forest			
Richness (*S*, species number)	41.2	6	2.534*
Diversity (H')	41	10	9.988***
Overall abundance (no. ind./kg litter)	0.4	–	1.482
Pine forest			
Richness (*S*, species number)	75	3	2.226*
Diversity (H')	92.6	3	6.485***
Overall abundance (no. ind./kg litter)	19.1	–	1.442

Distance contrasts performed through Helmert tests (analysis of variance, $\alpha = 0.05$; reference level at 1 m within edge; 7 df). ***$p < 0.001$; *$p < 0.05$. Threshold distances (beyond which no further change was statistically detected) and the mean percentage of net variation between 1 and 100 m from the road edge are shown.

Road edge effect in richness, parametric diversity and rarefaction

In the laurel forest there was a marked net reduction in richness and diversity in the immediate road vicinity (1 m) (transects mean ± DT; absolute species number, $S = 10 \pm 8$ species, Shannon's $H' = 1.7 \pm 0.61$) compared with 100 m toward the interior ($S = 17 \pm 7$ species, $H' = 2.88 \pm 0.37$). In laurel forest, and from road to interior, weighted species richness increased steeply up to a maximum at 6 m (18 ± 6 species/kg·litter), and Shannon's diversity reached an asymptote at 10 m from the edge ($H' = 2.70 \pm 0.41$). Neither richness nor diversity showed statistically significant change beyond these thresholds (Figure 4, Table 1).

In the pine forest, both richness and diversity at 1 m (transects mean ± DT; absolute species number, $S = 0.75 \pm 0.85$; $H' = 0.135 \pm 0.26$) were significantly lower than at 100 m from the edge ($S = 3.75 \pm 3.32$; $H' = 1.76 \pm 0.97$). Maxima in weighted species richness were attained at 3 and 10 m from the edge (3 ± 3 species/kg·litter), whereas the maximum in H' appeared as far as 100 m from the edge. The monotonically increasing diversity along the full gradient suggests that the edge effect in diversity may still propagate beyond this distance. No overall significant trend was detected beyond the threshold for weighted richness, despite a new maximum reached at 100 m from the edge (Figure 4, Table 1).

Rarefaction plots revealed that species accumulation rates differed greatly both within and between forests (Figure 6). Higher rates of species accumulation were found next to the road edge (1–20 m) compared with greater distances (40–100 m) (Figure 6). The maximum in the rarified species richness was detected at 10 m from the road edge in both ecosystems (Figure 6), with the steepest gradient in species richness occurring in the laurel forest. In the pine forest, maximum species accumulation per individuals sampled was found at 10 and 100 m, and the minimum was found at 1 m from the edge.

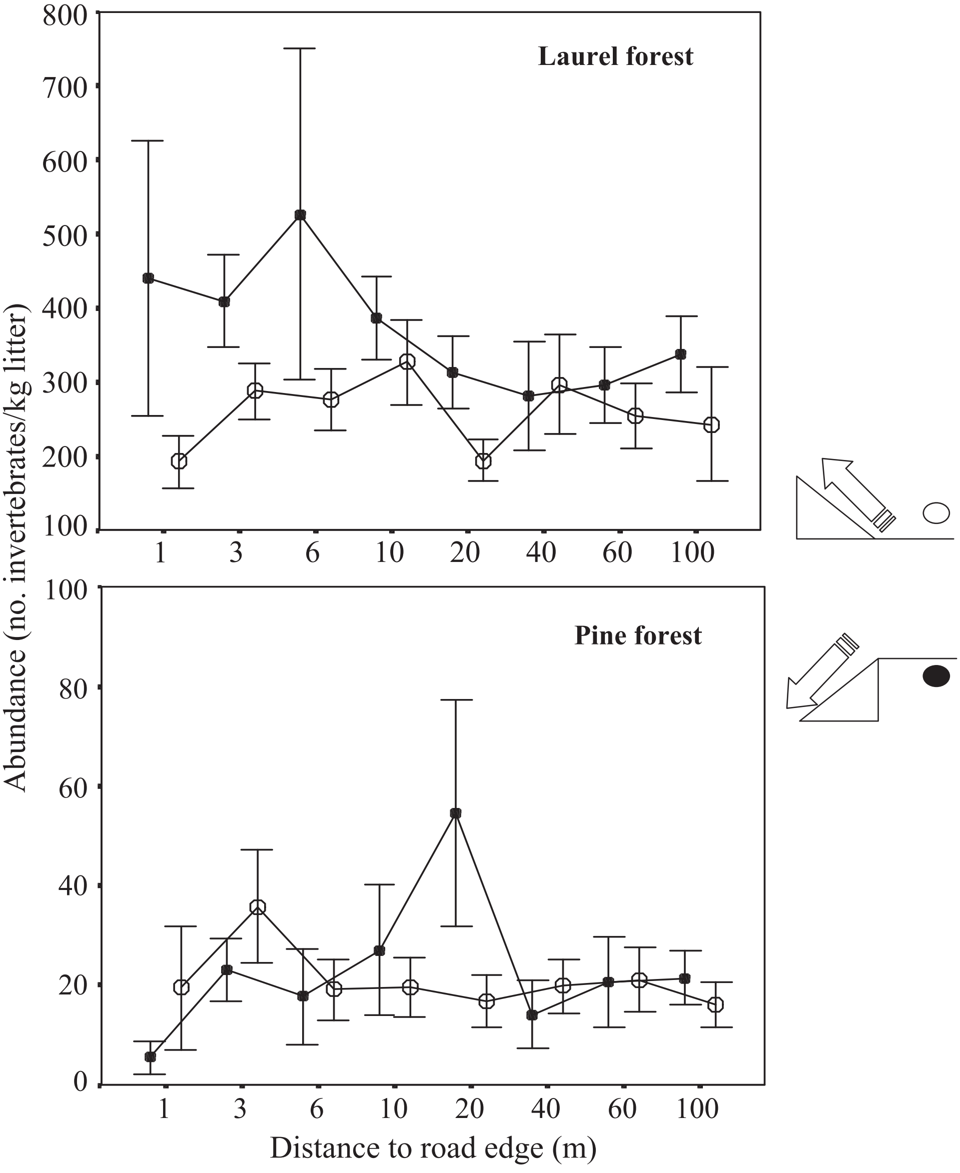

Figure 5. Relationship between distance to road edge and faunal abundance [mean (circles and dots) ± 1SE (vertical bars)]. Transects were divided depending on direction from road: "upslope" or above-road (open circles) versus "downslope" (black dots) or below-road attending to terrain profile.

The position of road edges within the topographic profile did not apparently affect species richness or diversity of invertebrates (Figure 5, Table 2).

Road edge effect in habitat predictors

Road edge effects on major stand structure and ground structural predictors are depicted in Figure 7. Necromass (litter or deposit biomass) and litter depth increased

Table 2. General linear model (analysis of variance) of effects of road proximity on abundance and diversity of litter fauna in laurel and pine forests.

		Abundance		Richness (*S*)		Diversity (*H′*)	
	df	SS	*F*	SS	*F*	SS	*F*
Laurel forest							
Corrected model	31	33.09	1.49	2825.67	2.15***	33.30	5.47***
Intersection	1	2855.29	3995.88***	25829.87	609.80***	636.34	3241.01***
DISTANCE	7	2.06	0.41	751.40	2.53*	13.73	9.99***
ROAD TYPE	1	0.70	0.97	42.12	0.99	0.09	0.45
LOCATION	1	3.61	5.05*	43.43	1.03	0.68	3.46
DISTANCE × ROAD TYPE	7	0.99	0.19	110.39	0.37	0.36	0.26
DISTANCE × LOCATION	7	0.64	0.13	193.58	0.65	0.17	0.12
DISTANCE × ROAD TYPE × LOCATION	7	1.77	0.36	443.05	1.49	0.14	0.10
Pine forest							
Corrected model	31	48.66	0.65	3.29	0.99	2.32	1.69*
Intersection	1	727.55	302.46***	28.48	267.33***	11.42	258.77***
DISTANCE	7	24.28	1.44	1.66	2.23*	1.61	5.21***
ROAD TYPE	1	0.96	0.40	0.15	1.36	0.00	0.003
LOCATION	1	0.07	0.028	0.02	0.17	0.04	0.88
DISTANCE × ROAD TYPE	7	10.91	0.648	0.58	0.78	0.15	0.49
DISTANCE × LOCATION	7	6.33	0.38	0.27	0.37	0.09	0.29
DISTANCE × ROAD TYPE × LOCATION	7	9.38	0.56	0.54	0.72	0.17	0.56

Factors: distance to road edge (DISTANCE), road type (ROAD TYPE: asphalt versus unpaved), location of transect regarding terrain profile (LOCATION: above versus below road), and interactions. SS = type III Sum of Squares; df = degrees of freedom; $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$.

toward the interior regardless of forest type. Moisture content showed an asymptote at 10 m from the edge in laurel forest and at 3 m in the pine forest, with overall levels being lower in the latter. Variation in percentage litter cover followed similar patterns in both forests, stabilizing at 10 m from the edge. Rock cover showed ample variation in both forests, being higher in pine forest. Grass and shrub cover were clearly higher at the road edge in laurel forest, and showed a more diffuse pattern in pine forest. In both ecosystems, canopy cover and height stabilized after approximately 10 m from the edge. Laurel forest canopy density levelled after 10 m from the edge. Richness of canopy-forming tree species in laurel forest varied widely along the whole gradient, but showed an increasing trend toward the interior forest. The canopy of the Canarian pine forest is almost monospecific with scattered treelets of *Erica arborea* and *Myrica faya*, and richness stabilized soon after the road edge. Vertical diversity of vegetation was greater and varied more widely in laurel than in pine forest.

Invertebrate species–habitat relationships: direct gradient analysis

The first two axes of the CCA explained 42.4% and 41.8% of the variation in laurel and pine forest, respectively. The analysis resulted in four axes explaining 66.7% and 69.9% of the variation in laurel and pine forests, respectively. Intensity of the gradients explained by the first axis in both forests was higher than for the second axis,

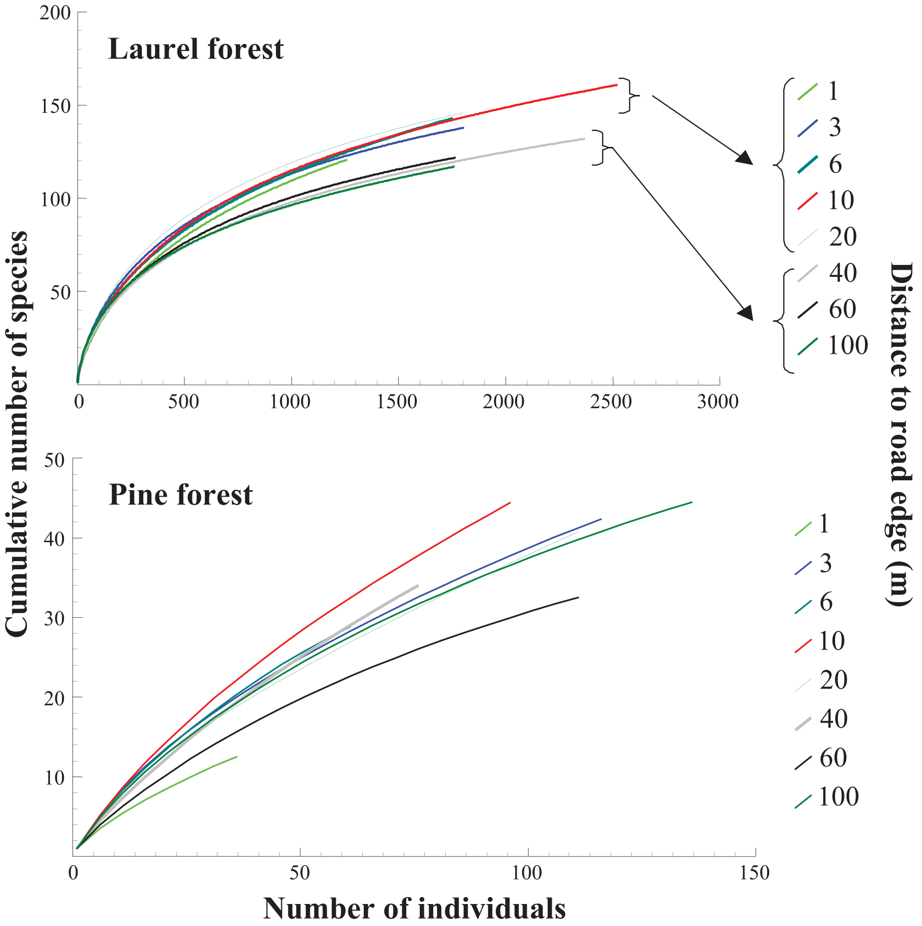

Figure 6. Rarefaction curves for road–interior transects in laurel and pine forest.

whereas total inertia was higher in the pine forest, as revealed by eigenvalues in Table 3. Correlations between species scores and the ordination axis were significant ($R^2 \sim 0.6$; $p < 0.05$; Table 3).

In the laurel forest, five variables (MOIST, LITTER, ROCK, DIST and NVSTRATA) had the most significant effect on the invertebrate community structure (Monte Carlo permutation test, $p < 0.001$) (Table 3, Figure 8). The first axis represented a gradient from low to high litter moist sites (MOIST). The second axis was related to the transition between road edge and forest core areas (Figure 8), which was in turn associated with a gradient in litter (LITTER) and rock (ROCK) cover. Variables negatively related to increasing distance to road edge (DIST) were herbaceous (HERB) and shrub cover (SHRUB). Litter cover, dry necromass (DRYWEIGHT) and litter depth (DEPTH) were strongly correlated and increased toward the interior. Distance to road edge correlated with higher canopy cover (COVER) and tree species richness (TREES), factors that increased along axis 2 toward the interior.

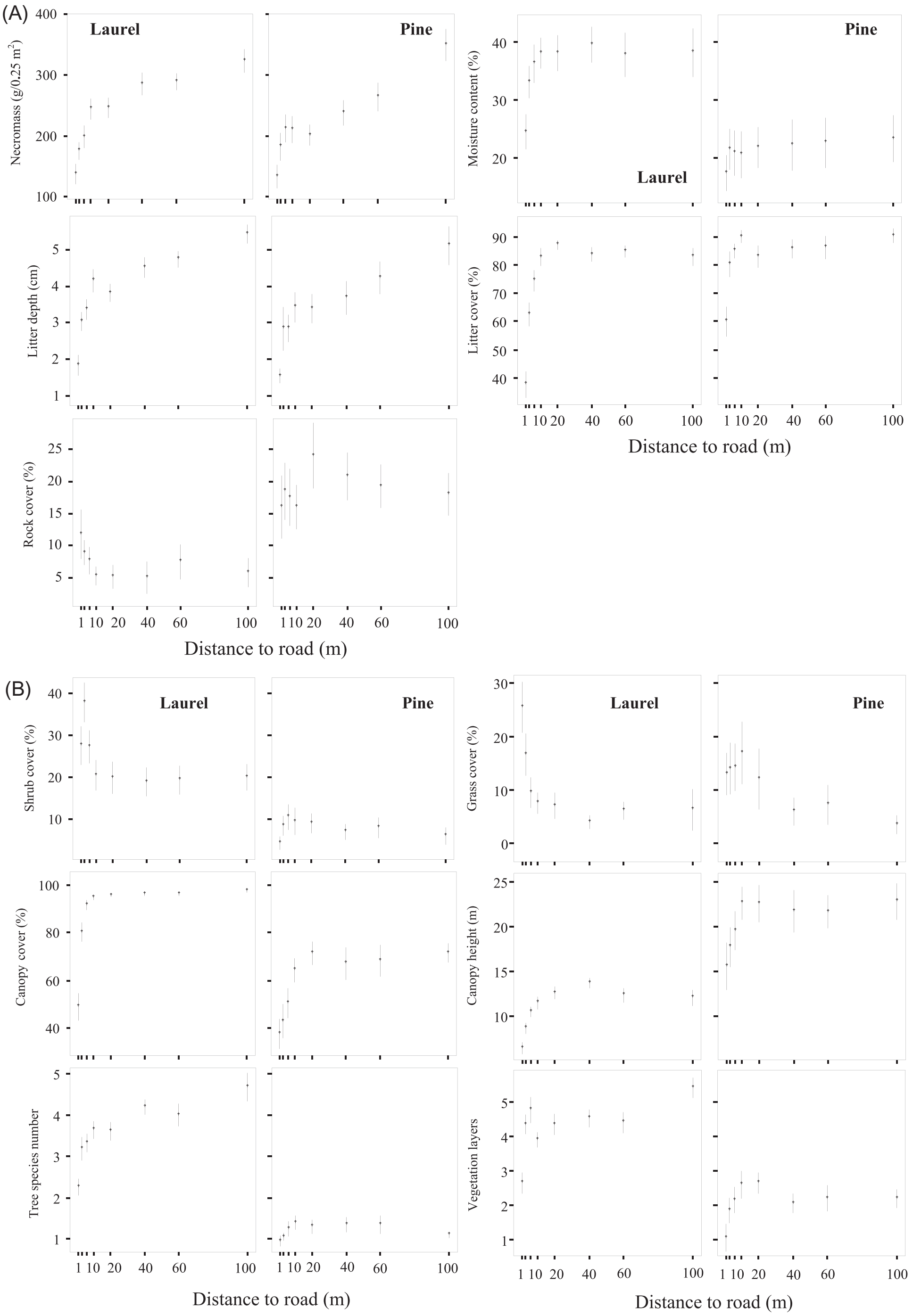

Figure 7. (A) Variation in substrate structure over the forest-road gradient. Means (dots) ± 1SE standard errors (vertical bars) are shown for each edge distance: 1, 3, 6, 10, 20, 40, 60 and 100 m. Necromass refers to dry leaf biomass and moisture content refers to leaf litter. (B) Variation in vegetation structure over the forest-road gradient. Means (dots) ± 1SE standard errors (vertical bars) are shown for each edge distance: 1, 3, 6, 10, 20, 40, 60 and 100 m.

Table 3. Canonical correspondence analysis of species–habitat relationships in the invertebrate litter community in laurel and pine forests.

		Laurel forest		Pine forest	
		Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues		0.085	0.048	0.233	0.167
% cumulative variance		27	42.4	24.4	41.8
Species–habitat relationships		0.639	0.604	0.7	0.627
Results of Monte Carlo permutation tests	Variable code	*F*		*F*	
% litter moisture	MOIST	4.77***		1.91	
% litter cover	LITTER	4.20***		1.12	
% rock cover	ROCK	3.68***		1.42	
Distance to road edge (m)	DIST	2.44***		1.66	
No. of vertical vegetation strata	NVSTRATA	1.94*		0.69	
% herbaceous cover	HERB	2.18		2.86***	
% canopy cover	COVER	1.22		2.9***	
Litter depth (cm)	DEPTH	1.98		1.27	
Canopy height (m)	HEIGHT	1.72		1.74	
% shrub cover	SHRUB	1.55		1.40	
Litter dry weight (g)	DRYWEIGHT	1.51		1.42	
No. of tree species †	TREES	1.63		–	

Significance of Monte Carlo permutation tests (500 permutations) for predictor variables: **$p < 0.01$; *$p < 0.05$. All species–habitat correlations significant at $\alpha = 0.05$.
†Variable not computed for the pine forest.

In laurel forest, rock cover was correlated with axis 1. It was not significantly dependent on distance to roads, but was negatively correlated with moisture content and positively associated with grass and shrub cover. Rock cover was the third factor by order of importance in determining species–habitat relationships (Figure 8).

In the pine forest, two variables (COVER and HERB) had a significant influence (Monte Carlo permutation test, $p < 0.001$; Table 3, Figure 8). Tree and grass cover had similar scores on both axes. Axis 2 was related to the road–interior gradient, although not significantly. There was an association between distance to road edge and litter moisture. The best associations were found among canopy descriptors COVER, NVSTRATA and HEIGHT. The distance to road edge had a much smaller effect on litter community changes in pine than in laurel forest, supporting what rarefaction and parametric diversity indices had already suggested.

Discussion

Road edge effects and disturbance gradients

This study documents changes in composition, abundance, richness and diversity of the litter invertebrate communities in laurel and pine forests fragmented by asphalt

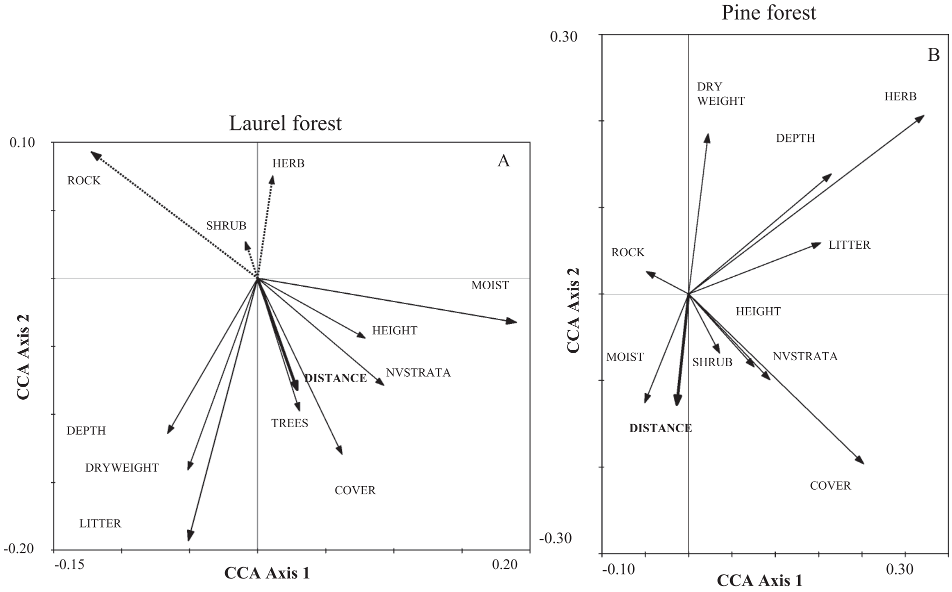

Figure 8. Canonical correspondence analysis for the species–habitat relationships within the plane defined by the first two ordination axes. Road proximity (Distance) is highlighted. Arrows indicate the direction of the most intense change in the variable of interest; arrow length reveals the importance of the variable in community structure and its predictive capacity; arrow direction indicates its degree of association with the relevant composite gradient (the respective axis); angles among arrows indicate the correlation among variables (the smaller the angle, the tighter the association). For the laurel forest: dotted arrows, variables with a higher degree of association to the road edge; continuous arrows, variables with a higher degree of association to the forest "core-like" conditions. Variable codes as in Table 3. Percentage variance explained in Table 3.

and unpaved roads. The road edge effect did not depend significantly on road type in either forest. Richness and diversity increased abruptly and reached a peak within ~10 m from road edge. Abundance increased also within the first 10 m from the edge, although no statistically significant trend accounted for this effect. In the species-rich laurel forest, diversity did not fluctuate significantly beyond this distance, where "background" forest conditions were apparently attained. Such an apparent threshold of disturbance of the road gap was consistently shown by both rarefaction and parametric indices. In fact, rarefaction results were not only consistent with species richness and parametric diversity for the laurel forest, but also with the absence of a clearer pattern for the pine forest.

Roadside habitats are often considered as ecotones, i.e. a discrete zone where the rate of environmental and biotic change are the highest (Fortin 1994), and where differential abundance, composition of the species assemblage, and richness occur (Forman and Godron 1986; Yahner 1988). The changes in taxonomical composition and biodiversity were related to steep gradients in forest microclimate and structural conditions occurring on this narrow band parallel to both asphalt and unpaved roads, patterns already reported for microclimate and vegetation structure in these island forests (soil, litter and air temperature, light incidence, canopy height and cover; Delgado et al. 2007b; Arévalo et al. 2008, 2010).

Road edges in these forests, as in any other habitat frontier, are not fixed and steady structures, but are highly dynamic. Several factors could delineate more explicitly the road–forest buffer (e.g. Forman et al. 2002), and so determine rates of taxonomic change, richness, diversity and abundance of the epifauna. Potentially important factors not examined here include motorized traffic intensity, pollutant dispersal, road age (date of construction), substrate erosion along edges, degree of alien plant occupation (Munch 1993; Arévalo et al. 2008, 2010; Arteaga et al. 2009; Alexander et al. 2011), wind regimen and direction, soil depth and type, and chemical (and allelochemical) diversity of the leaf litter environment, among others (Spencer and Port 1988; Forman and Alexander 1998; Spellerberg 1998).

Ordination analysis revealed strong gradients in ground and stand-level variables, namely litter moisture content, litter, rock and canopy cover in the laurel forest, and in litter and rock cover, litter moisture and weight in the pine forest. Our results with litter invertebrates suggest that the highest invertebrate richness and parametric diversity were consistently attained at intermediate distances from road edges, where variation in forest structure departed from the extremes of both interior forest and road gap. Biotic diversity is assumed to peak at intermediate disturbance levels (Connell 1978). Roads in our study forests induce steep disturbance gradients, including impact on alien vertebrate predators (i.e. rats; animal and plant predator; Delgado et al. 2001b) and native seed dispersers (i.e. endemic *Gallotia* lizards and birds, Delgado et al. 2007a; Delgado et al. 2008). In the laurel forest, changes in these parameters in the forest interior were less intense, subordinated to the local formation of canopy gaps, which were relatively uncommon, making the forest interior a more stable environment (Arévalo and Fernández-Palacios 1998; Arévalo et al. 2008). Both microclimate (Delgado et al. 2007b) and canopy gradients were clearly steeper in laurel than in pine forest. In addition, the contrast in richness between edge and interior communities was less noticeable in the pine than in the laurel forest. This would be a result of the lower overall richness and abundance in pine forest, explained by its comparatively harsher environment.

Functional and structural implications of road edge effects for forest litter fauna

The road edge community of Canarian forests is a strongly transformed community whose composition, diversity and environmental conditions are in sharp contrast with that of sheltered interior areas. A wide variety of sun-loving endemic plant taxa, typical of forest gaps, takes advantage of the road-induced gaps. Here, lower and sparser canopy cover, increased desiccation, increased light and changed light regimens (i.e. higher variability of the light environment near the road edge in both laurel and pine forests; Delgado et al. 2007b), and litter fall may have a strong influence in both litter and soil fauna. For instance, we have shown here that road situation within the topographical context affects the litter community composition and abundance. Leaf litter accumulation is higher downslope along road edges, causing local peaks of invertebrate abundance and richness on the road edge zone. Over wide landscape scales, this would involve serious implications for planning, design and management of roads. In sloping forest terrain typical of most mountainous islands, roads might interact with slope and topography to introduce strong asymmetries in biogeochemical and biotic processes in otherwise continuous habitats. Efforts should be devoted to assess this disturbance at the regional island level.

The road effect zone has a determinant role in the ecological dynamics of the top layer of forest soils, shaping the distribution and composition of the invertebrate communities. The disturbance effect of the road on the soil properties and community is directed and chronic (see Giller 1996). From the gap opened in the forest canopy, and the artificial substrate that forms the road corridor, derive several interacting gradients (light, water and moisture, wind and chemical and pollutant levels), affecting soil structure and desiccation, the above-ground plant biomass and hence the amount of buffering litter (necromass) produced. Although the forest soil is a highly stable environment (Giller 1996), different factors introduce wide spatial heterogeneity.

Ecological and biogeochemical processes can be severely disturbed by roads, as far as key species are affected, as we suggest for litter invertebrates [pollinators (Lepidoptera, Diptera recorded in our work mostly in larval forms, Hymenoptera and Coleoptera), decomposers or deposit feeders (earthworms, land snails, crustaceans such as isopods, myriapods)]. In the laurel and pine forests, this work reveals that a critical component of the trophic chains, the detritivorous guild, are severely pervaded by overabundant, invasive alien species, which contribute to the overall abundance of detritivorous species along road edges. Despite this, we still lack a good knowledge of the functional effects (or lack of effect) of such dominant aliens like invasive millipedes (*Ommatoiulus*, *Brachydesmus* and others) (see Enghoff and Báez 1993), isopods (*Armadillidium*, *Eluma*) (Arndt and Perner 2008), earthworms (*Eisenia*) (Talavera 1987) or ants (Farji-Brener and Ghermandi 2008).

The fauna associated with the native vegetation could also be affected by road disturbance through the facilitation of some epiphytic alien taxa. Fragmentation along road edges may also interrupt the communication between canopy and ground faunal compartments. Under low canopies (such as 2–5 m height, this study, see Figure 7) prevailing at road edges, typical canopy species would be prone, or forced, to use the ground more frequently (Foggo et al. 2001). This would increase the number of canopy species forced to enter and enrich the litter community. Along with ground species coming through the road corridor, such canopy dwellers are potentially important contributors to the roadside fauna and to the increased richness of such edge habitats (Davis and Sutton 1998). Unfortunately, for a serious comparison between canopy and ground compartments, we lack information on the composition of canopy invertebrate species for both laurel and pine forest in the Canary Islands, and we did not attempt to gather such information in this study.

Some authors have detected higher diversity of carabid beetles along forest edges and adjacent grassland than in forest interiors (e.g. oak–hornbeam, Magura et al. 2001). In such forest–non-forest interfaces, increases in species diversity at the edge are commonly the result of contributions from adjacent habitats. In our study system, and in other forest roads worldwide, the road was the prevailing edge habitat at the landscape scale, and so acted as the “adjacent habitat”. The road right-of-way can favour the entrance of species that would use road habitats intensely (which is our case with aliens like *Ommatoiulus moreletti* or native generalists, such as *Eluma purpurascens* or *Armadillidium vulgare*, as well as some alien and native ants).

Alteration of productivity along edges may trigger the decline of invertebrate species in fragmented forests, and the reverse could be true (Didham et al. 1998). Necromass accumulation depends on a combination of factors, such as species type, net primary production, ground decomposition rates and seasonality. Increased falling rates of vegetative (leaf), reproductive (flowers) and support material may take place along roads through wind, vehicle disturbance and altered productivity, among other factors (Forman et al. 2002 and references therein). Haskell (2000) also suggested that an edge effect in litter depth would be partially responsible for reductions in invertebrate abundance near roads.

In the laurel forest, great monthly variation occurs in litter production along the road–interior gradient (Arévalo et al. 2008), although with no clear seasonal rhythms in senescence, fruit production or leaf loss due to the tropical affinities of the palaeoendemic tree species (Fernández-Palacios 2009). Arévalo et al. (2008) reported decreased litter deposition along road edges in laurel forest, and stabilization after 10 m from the road edge.

We found that the litter layer was significantly shallower near the road edge. This might be related to a lower, less dense and less complex edge canopy, higher cover of a bush layer of perennial shrubs and young trees, grasses and herbs which, combined, produce much less necromass than the interior mature canopy (Figure 7). Supporting this suggestion is the selection of the variable number of vertical vegetation layers along the road edge (NVSTRATA) as a significant predictor in the invertebrate community of laurel forest (Table 3).

Changes induced by roads (i.e. disturbance) on floristic composition are partially translated into functional changes (e.g. productivity and litter conditions, chiefly litter moisture, cover and depth) and, hence, on the associated litter and soil animal communities. Considering the whole invertebrate assemblage, litter and, in general, ground structural variables were the most determinant in laurel forest, whereas herb and canopy cover were relevant on the more simple structure and composition of the pine forest (Table 3).

Furthermore, differences in litter fauna between these two forests can be related to the intrinsic properties of their ground microhabitat, as a probable consequence of their contrasting composition and structure. Although general patterns of edge-to-interior variation in necromass deposition, litter depth and cover are not very different between laurel and pine forests (i.e. overall necromass deposition rates are similar between forests, $\sim$1 kg m^{-2} year^{-1}, Fernández-Palacios et al. 1992), there is evident contrast in other fine-grained determinants for invertebrates such as rocky cover (higher in the pine forest) and litter moisture (higher in laurel forest) (Marsh and Beckman 2004; Kappes et al. 2009).

The physical structure of the edge may determine the gradient in microclimate between road edge and forest interior (Chen and Franklin 1992; Chen et al. 1993; Forman 1998; Honnay et al. 2002). In our system, environmental conditions in the pine forest are harsher than in the laurel forest. This can be a confounding influence because climate harshness can exceed in intensity the local effects of roads. This can be a reason for the relatively diluted effect of the road observed in the pine forest, causing apparently gentler gradients in the litter community.

In both forests, light incidence, and air, soil and litter temperature are steeply reduced whereas litter moisture increases from both asphalt and unpaved roads to the first 10 m of forest, stabilizing thereafter (Delgado et al. 2007b; this study). Beyond a narrow road-buffer band (10-m width) other factors like microtopography, aspect and canopy tree species composition (causing differential leaf litter chemical composition) may play an influential role on the litter community. In the laurel forest, there is a remarkable coincidence between the light incidence distance and the peak in invertebrate diversity, the maximum of rarefied richness. This is also supported by numerous modal values at 10 m from the edge found in the distributions of many species from disparate taxa (unpublished data).

The variables studied here explain a significant amount of variance in composition and abundance of invertebrates. Other variables such as roadside management practices (Gonseth 1992) and spatio-temporal heterogeneity, could partially account for the remaining unexplained variance. Giller (1996) and Scheu and Schulz (1996) have found important effects on litter invertebrates of species–nutrient relationships, soil vertical structure, litter allelochemicals and fungal and bacterial biota, among others.

Patterns of change of abundance, richness and diversity

In other fragmented ecosystems, different edge types have been related to variable distances of propagation of edge effects. In forested ridge tops on acidic soils, snail taxonomic composition differed between calcareous roadsides and the interior, and dry mass of both snails and millipedes decreased significantly from road to interior, although abundance was unaffected (Kalisz and Powell 2003). Didham et al. (1998) found that the beetle fauna was affected up to 105–210 m from the edges of Amazonian rainforest fragments. Analysing overall patterns of road edge effects on soil macrofauna on Appalachian forests, Haskell (2000) found that invertebrate abundance and richness at the order or class levels, and litter depth, decreased near relatively narrow, unpaved roads up to 15–100 m toward forest interiors. Major orders such as Chilopoda, Acari, Araneae and Coleoptera revealed significant decreases near the road edge.

Responses at the community level would be the result of the combined responses of particular taxa. The magnitude of edge effects on invertebrates could be underestimated with taxonomic levels higher than species or genus (Hammond 1994; Oliver and Beattie 1996). Species in the same order or even the same genus could differ greatly in their responses to edge effects, even showing opposite responses (see Didham et al. 1998). It is important to consider which species participate in abundance, and in what proportions, because low taxonomic resolution hampers the detection of critical thresholds in road edge effects on extremely rich ground invertebrate assemblages.

There was a clear dominance of alien and non-endemic native species in the leaf litter community of both forests. This is a further reason to prefer studies developed at the species or morphospecies level instead of surveys at higher orders on fragmented ecosystems. Edge effects measured at the whole assemblage level could be strongly dependent on the responses of a few but overabundant generalist taxa, so they might be hiding fine-grained effects of roads, such as responses of invasive species with requirements for non-disturbed or, on the other hand, disturbed habitat (Arndt and Perner 2008).

Species turnover rates (β-diversity) along the edge–interior transition are probably high in both forests. This may be related to a very rapid initial change in biodiversity on the first few meters from the asphalt or dust edge toward the interior. Such high turnover rates are consistent with predictions of the classical niche theory: a higher biodiversity would result in comparatively reduced and more specialized niches with a higher degree of resource partitioning (Giller 1996). This higher biodiversity must be understood at least in part as a result of the differential contribution of non-native species along road edges, especially within the first few metres from the road surface. In such a transformed road–forest buffer, factors positively affecting species richness may also promote invasibility (Kappes et al. 2009). In addition, in the laurel forest, the richness of canopy-forming tree species increased towards the forest interior (Figure 7). This would affect the leaf-litter chemical composition and structure, and have an indirect effect on the fauna occupying ground and above-ground biotic compartments, probably increasing diversity of native invertebrate taxa and limiting the potential for alien species to establish (Arndt and Perner 2008).

In the laurel forest, the net difference between the extremes of the gradient was negligible for global species richness but it reached 59% for the Shannon index of diversity. Hence, a better knowledge can be gained by measuring disturbance effects through species turnover rates (and unbiased methods like rarefaction) than with parametric indices, especially given that totally different species pools may render the same or very similar parametric richness and diversity from edge and interior situations.

In conclusion, road fragmentation in the invertebrate litter communities on these forests caused an edge effect whose main implications are: (1) short and abrupt road edge buffers in both forests, where composition, richness and abundance of the invertebrates are strongly modified patterns explained by road alteration of habitat structure; this could imply a functional reduction of ecosystem area due to disturbance from roads, that accumulates at a regional landscape level; (2) a consistent increase of richness/diversity within the first ~ 10 m from the edge towards the forest interior; this effect is consistent with the predictions of general niche theory and seems to give some empirical support to the intermediate disturbance hypothesis; (3) an increase in abundance in favour of a few alien and generalist native species with an increase of their abundance in a band or buffer near the road edge. Regarding the introduced alien species, we should determine whether they are involved in processes triggering further changes to the island's biodiversity, with species loss (mostly natives and endemics) and gains (mostly non-native invaders), through changes in species interactions (competence, predation and displacement of local species).

Acknowledgements

We thank the following people for their assistance, identifying invertebrate species and/or providing useful keys and advice: Dr Manuel Baena, Córdoba, Spain (Hemiptera); Dr Marcos Báez, Dept. Zoología, Universidad de La Laguna, Tenerife, Canary Islands, Spain (DZUL) (Diptera, Lepidoptera, Heteroptera and others); Dr Arturo Baz, Dept. Biología Animal, Universidad de Alcalá, Spain (Psocoptera); Dr Hermans Contreras (DZUL) (Coleoptera); Dr Henrikk Enghoff, Entomological Department, Zoological Museum, University of Copenhagen, Denmark (Miriapoda: Diplopoda); Dr Xavier Espadaler, C.R.E.A.F., Universitat Autònoma de Barcelona, Spain (Hymenoptera: Formicidae); Dr Miguel Gaju Ricart, Dept. de Zoología, Universidad de Córdoba, Spain (Archaeognatha: Thysanura); Dr Miguel Ibáñez, DZUL (Mollusca: Gastropoda); Dr Francisco La Roche, DZUL (Himenoptera); Dr Antonio Machado, Dept. de Ecología, Universidad de La Laguna (Coleoptera, especially *Laparocerus*); Dr Volker Mahnert, Geneva, Switzerland (Pseudoscorpiones); Dr Pedro Oromí, DZUL (Arthropods in general, Coleoptera); Dr Gloria Ortega, Museo de Ciencias Naturales de Tenerife (Himenoptera: Aculeata). Gloria García helped with field work. This work was done partly within the project "Impacto de los corredores antrópicos sobre los invertebrados de la laurisilva y el pinar de Tenerife", funded to Juan D. Delgado by "Gestión y Planeamiento Territorial y Medioambiental, S.A." (GesPlan) and the "Viceconsejería de Medio Ambiente, Gobierno de Canarias".

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Appendix 1. Location and description of road–interior transects in laurel and pine forests in Tenerife (Canary Islands).
Road type: A = Asphalt road; U = unpaved road or track. Road width includes edges plus zones accessible by vehicle

Transect	Forest	Locality name	UTM (28RCS)	Road type	Aspect	Elevation (m a.s.l.)	Road width (m)	% Canopy cover above road
1	Laurel	Las Mercedes-1 (Anaga)	0373402; 3157012	A	W	800	8.2	57.4
2		El Moquinal-1 (Anaga)	0372281; 3157803	U	NW	750	7	0
3		Hija Cambada (Anaga)	0374348; 3157158	A	N	850	9.3	12.6
4		Pico del Inglés-1 (Anaga)	0375505; 3157505	A	SW	980	7.7	0
5		Cruz de Fune-Las Lagunetas (Tacoronte)	0362603; 3147754	U	NE	1050	5	45.9
6		La Hornaca (Tacoronte)	0363413; 3147957	U	N	990	4.6	56.3
7		Las Yedras-1 (Anaga)	0375205; 3157445	U	NE	800	3	12.6
8		Las Quebradas-1 (Anaga)	0380191; 3157653	A	NE	770	7	48
9		Las Mercedes-2 (Anaga)	0375850; 3156746	A	NNE	840	7.8	0
10		Casa Forestal Cruz del Carmen (Anaga)	0373339; 3157064	U	NE	850	4.3	67.8
11		Cruce Los Batanes (Anaga)	0372827; 3157187	A	NE	790	5	8.5
12		Pico del Inglés-2 (Anaga)	0375644; 3157353	A	NW	880	8.7	9.5
13		Monte del Agua-1 (Teno)	0320805; 3135696	U	NW	790	6	16.8
14		Monte del Agua-2 (Teno)	0321236; 3134329	U	E	840	11.5	0
15		Inchires (Anaga)	0379470; 3157644	A	SE	730	7.2	0
16		Pico del Inglés-3 (Anaga)	0375225; 3157057	A	S	980	6.4	0
17		Santa Úrsula-1 (Reserva de Las Palomas)	0356488; 3142955	U	NNW	950	5.5	0
18		Santa Úrsula-2 (Reserva de Las Palomas)	0356845; 3142975	U	N	990	4.7	21
19		Santa Úrsula-3 (Las Cabezadas)	0357855; 3143659	U	N	955	4.2	39.7

(*Continued*)

Appendix 1. (Continued).

Transect	Forest	Locality name	UTM (28RCS)	Road type	Aspect	Elevation (m a.s.l.)	Road width (m)	% Canopy cover above road
20		La Vica (La Matanza)	0360305; 3146555	U	W	880	3.7	43.8
21		Ladera de Tigaiga (Los Realejos)	0344425; 3136930	U	N	1090	5.5	3.3
22		Pico del Inglés-4 (Anaga)	0375053; 3156944	A	NNW	860	6.4	0
23		El Pijaral-1 (Anaga)	0384250; 3158811	A	SEE	720	6.3	6.4
24		Cruz del Carmen (Anaga)	0374140; 3156601	A	SW	805	6	29.3
25		Pedro Álvarez (Tegueste)	0372869; 3156629	A	SE	755	6.5	26.2
26		Cruz de Afur (Anaga)	0375999; 3157072	A	SW	989	6.8	33.4
27		El Pijaral-2 (Anaga)	0384054; 3158721	A	S	740	5	29.3
28		Las Yedras-2 (Anaga)	0373585; 3157205	U	N	820	3.2	57.4
29		El Bailadero	0382455; 3158445	A	N	600	7	75
30		Cruce pista Cruz del Carmen	0373355; 3157153	A	N	850	11	0
31		Casas de Viñátigo	0375775; 3157595	A	N	930	7.6	0
1	Pine	Los Ovejeros-1	0362199; 3157599	U	S	1025	7.5	4.3
2		La Esperanza-1	0364682; 3145383	A	SW	1080	8.6	25.1
3		Las Lagunetas-1	0365550; 3144505	A	SE	1400	7.5	79.2
4		La Esperanza-2	0363095; 3144618	A	NW	1340	7.5	57.4
5		Morada del Viento (La Victoria)	0361286; 3143715	A	NNW	1470	6.1	55.3
6		Vilaflor-El Pinalito	0333925; 3117432	A	NNE	1575	8	27.2
7		Las Lagunetas-2	0362750; 3143989	A	N	1260	7.6	56.3
8		Los Ovejeros-2	0363717; 3144038	U	SES	1030	7.5	48
9		Barranco Hondo	0364380; 3143385	U	SSE	1030	3.8	43.8
10		Siete Fuentes	0360565; 3143520	U	N	1460	6.3	9.5
11		Montaña Grande-1	0364440; 3145145	A	SEE	1100	8.6	24.1

(*Continued*)

Appendix 1. (Continued).

12	Barranco de La Arena (La Guancha)	0334050; 3135551	U	N	1080	9.5	0
13	Las Raíces	0365245; 3145075	A	E	1065	13.4	12.6
14	Montaña Grande-2	0365050; 3145310	A	SE	1150	8.5	11.6
15	Arico, Altos del Contador	0348295; 3121098	U	SE	1555	7	0
16	Granadilla, El Río	0344146; 3118311	U	S	1560	6.5	1
17	Altos de La Victoria	0360552; 3142555	A	N	1690	7.2	2
18	Los Ovejeros-3	0363655; 3144005	U	SE	1100	7	17.8
19	Campamento Emilio Fernández Muñoz (Realejos)	0343355; 3135445	U	N	1600	4.7	18.9
20	Altos de Arafo	0358355; 3140550	A	E	1670	9.5	0

Appendix 2. Average density (no. of individuals/kg dry litter) of invertebrate orders at every distance interval to road edge in the Tenerife laurel forest

Phyla	Order	Distance to road edge (m)								No. of individuals	Overall density
		1	3	6	10	20	40	60	100		
Platyhelminthes	Tricladida				0.52					4	0.52
Nematoda	Undetermined					0.25			0.15	3	0.41
Annelida	Haplotaxida	20.84	38.02	28.05	69.60	18.36	21.49	23.73	43.61	1771	263.71
Mollusca	Stylommatophora	8.42	27.60	25.31	19.98	23.56	23.94	13.99	18.56	1099	161.36
Arthropoda	Pseudoscorpiones	0.22	2.74	1.45	0.91	1.65	0.93	1.57	2.78	81	12.26
	Opiliones	0.89	0.73	0.32	0.65	0.38	0.23	0.79	0.46	28	4.46
	Acari	0.44	3.29	1.61	3.26	2.41	0.93	2.04	3.40	117	17.40
	Araneae	10.42	15.72	12.09	10.32	10.13	5.84	6.76	11.60	535	82.88
	Isopoda	102.41	77.69	64.97	43.75	39.52	64.35	37.88	31.55	2933	462.12
	Amphipoda	0.67	1.65	2.42	0.78	0.89	1.52	1.57		63	9.49
	Polyxenida	1.11		1.29	3.79	2.03	0.93	0.31	1.08	75	10.54
	Polydesmida	39.46	42.41	29.18	45.71	28.37	38.66	30.49	38.66	1940	292.94
	Polyzoniida		0.18	0.48	0.52	0.13	0.12	0.16		11	1.59
	Julida	19.73	29.98	30.63	35.39	21.91	16.23	26.25	17.63	1307	197.75
	Scolopendromorpha		0.37	0.48	1.04	0.13	0.82	0.47	1.24	32	4.55
	Geophilomorpha	2.44	7.13	9.67	8.62	9.63	9.34	13.20	12.22	495	72.25
	Poduromorpha				0.13		0.47	0.16	4.95	38	5.70
	Entomobryomorpha	4.21	6.03	1.29	3.53	3.42	1.64	1.26	0.31	138	21.68
	Diplura		1.10	0.97	0.78	0.13	0.12		0.31	22	3.40
	Archaeognatha		0.55	0.97	0.52	0.51	1.52	1.57	1.70	51	7.34
	Zygentoma		0.18						0.31	3	0.49
	Blattaria	1.11	1.65	0.81	0.91	0.51	0.82	0.63	1.24	49	7.66

(*Continued*)

Appendix 2. (Continued).

	Dermaptera	0.44				0.13	0.12			4	0.69
	Psocoptera	0.22				0.63	0.12	0.16		8	1.13
	Hemiptera	8.65	22.30	20.31	20.37	17.10	29.55	39.29	19.79	1209	177.37
	Planipennia		0.18							1	0.18
	Coleoptera	34.80	34.00	34.66	37.61	29.00	36.56	43.85	37.73	1911	288.22
	Lepidoptera	5.76	1.83	0.97	3.26	4.43	3.27	6.44	10.05	236	36.02
	Diptera	2.66	4.02	5.48	6.14	5.19	4.44	4.40	2.32	237	34.65
	Hymenoptera	12.41	3.47	1.93	2.61	0.63	0.58	0.47	0.15	121	22.28
	Undetermined (larvae)	2.88	7.86	8.06	9.01	7.35	12.38	20.59	10.52	538	78.65
	Overall density	280.19	330.70	283.41	329.74	228.36	276.91	278.04	272.32	15,060	2279.68

Appendix 3. Average density (no. of individuals/kg dry litter) of invertebrate orders at every distance interval to road edge in the Tenerife pine forest

Phyla	Order	Distance to road edge (m)								No. of individuals	Overall density
		1	3	6	10	20	40	60	100		
Annelida	Haplotaxida	1.13	5.77	0.94	1.90	0.74	0.21	0.57	0.57	47	11.83
Mollusca	Stylommatophora	0.38	2.20	2.59	1.66	1.24	0.42	1.32	0.57	45	10.39
Arthropoda	Pseudoscorpiones					2.23	0.21		0.14	11	2.59
	Opiliones	0.38				0.25			0.14	3	0.77
	Acari		0.27	0.47						3	0.75
	Araneae	0.38	6.04	2.12	2.61	2.98	1.26	2.65	3.86	102	21.90
	Isopoda		0.55		0.24	0.50	0.84	0.19	2.29	26	4.60
	Polyxenida						0.21		0.14	2	0.35
	Polydesmida		1.92	0.24						8	2.16
	Julida	7.92	6.31	3.54	5.46	4.97	6.52	10.40	5.43	226	50.55
	Geophilomorpha				0.24		0.42	0.57		6	1.23
	Entomobryomorpha	1.51	1.37	0.24		0.25	0.21		0.57	16	4.15
	Archaeognatha		0.27		0.24	0.25	0.63	0.38	0.14	9	1.91
	Zygentoma		0.27	0.71	0.24	0.25			0.29	8	1.75
	Blattaria		0.27							1	0.27
	Psocoptera	0.38	0.27	0.47	0.24		0.21		0.14	7	1.71
	Hemiptera		1.10		1.19	1.74	0.21	0.19	1.00	25	5.42
	Planipennia					0.25				1	0.25
	Coleoptera	1.89	3.57	1.65	3.32	4.97	2.52	0.95	3.15	98	22.01
	Trichoptera				0.47	0.25		0.38		5	1.10
	Lepidoptera		1.10	0.71	1.90	0.25	0.42			18	4.37
	Diptera	0.38	0.55	0.71	2.14	1.99	0.63	1.89	1.00	43	9.28
	Hymenoptera			0.94			0.42	0.38		8	1.74
	Undetermined (larvae)		0.82		1.42	4.72	1.26	1.70	0.43	46	10.36
	Overall density	14.33	32.67	15.32	23.26	27.81	16.61	21.56	19.87	764	171.43