Distributional patterns of endemic, native and alien species along a roadside elevation gradient in Tenerife, Canary Islands

Giovanni Bacaro[1], Simona Maccherini[2], Alessandro Chiarucci[3], Anke Jentsch[4], Duccio Rocchini[5], Dino Torri[6], Margherita Gioria[7], Tordoni Enrico[1], Stefano Martellos[1], Alfredo Altobelli[1], Rudiger Otto[8], Carlos G. Escudero[8], Silvia Fernandez-Lugo[8], José María Fernandez-Palacios[8], José Ramón Arévalo[8]

[1]Department of Life Sciences, University of Trieste, Via L. Giorgieri 10, 34127 Trieste, Italy

[2]BIOCONNET, Biodiversity and Conservation Network, Department of Environmental Science "G. Sarfatti", University of Siena, Via P.A. Mattioli 4, 53100 Siena, Italy

[3]Department of Biological, Geological and Environmental Sciences, *Alma Mater Studiorum* University of Bologna, Via Irnerio 42, 40126 Bologna, Italy

[4]Department of Disturbance Ecology, Bayreuth Centre for Ecology and Environmental Research BayCEER, University of Bayreuth, Universitaetsstrasse 30, D-95440 Bayreuth, Germany

[5]Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, Via E. Mach 1, 38010 S. Michele all'Adige (TN), Italy

[6]CNR-IRPI, Istituto di Ricerca per la Protezione Idrogeologica, Via Madonna Alta 126, 06128 Perugia, Italy

[7]Institute of Botany, The Czech Academy of Sciences, Zámek 1, CZ-252 43 Průhonice, Czech Republic

[8]Departamento Ecología, Universidad de La Laguna, La Laguna, 38206 Tenerife, Spain

Abstract

Invasion by alien plant species may be rapid and aggressive, causing erosion of local biodiversity. This is particularly true for islands, where natural and anthropogenic corridors promote the rapid spread of invasive plants. Despite evidence shows that corridors may facilitate plant invasions, how their importance in the spread of alien species varies along environmental gradients deserves more attention. Here, we addressed this issue by examining diversity patterns (species richness of endemic, native and alien species) along and across roads, along an elevation gradient ranging from sea-level up to 2050 m a.s.l. in Tenerife (Canary Islands, Spain), at multiple spatial scales. Species richness was assessed using a multi-scale sampling design consisting of 59 T-transects of 150 m x 2 m, along three major roads each placed along the whole elevation gradient. Each transect was composed of three sections of five plots each: Section 1 was located on the road edges, Section 2 at intermediate distance, and Section 3 far from the road edge, the latter representing the "native community" less affected by road-specific disturbance. The effect of elevation and distance from roadsides was evaluated for the three groups of species (endemic, native and alien species), using parametric and non-parametric regression analyses as well as additive diversity partitioning. Differences among roads explained the majority of the variation in alien species richness and composition. Patterns in alien species were also affected by elevation, with a decline in species richness with increasing elevation and no alien recorded at high elevations. Elevation was the most important factor determining patterns in endemic and native species. These findings confirm that climate filtering reflected in varying patterns along elevational gradients is an important determinant of alien species richness, which are not adapted to high elevations, while anthropogenic pressures may explain alien species richness at low elevation.

Keywords: Diversity partitioning, invasive species, plant species richness, MIREN, island biogeography, disturbance.

Introduction

The interest in examining the mechanisms underlying plant invasions and their impacts has increased exponentially over the past few decades, with the majority of studies focusing on low-elevation, highly disturbed ecosystems. Until recently, the majority of information on plant invasion focused on processes and impacts at low elevations. On the other hand, less attention was paid in understanding such processes in more pristine and high-elevation environments, where most of the world's protected areas are located (Pauchard et al. 2009). Mountain and island ecosystems are known to be particularly prone to invasions by alien species (e.g. Barni et al. 2012): the reason for island ecosystems to be highly susceptible and vulnerable to the intentional and unintentional introduction of invasive species include their comparatively low habitat diversity, their simplified trophic webs and high rates of endemism (Courchamp et al. 2003). Island communities have undergone long lasting processes of mutual evolution due to their isolation from other ecosystems (Steinbauer et al. 2013). Thus, island communities have not evolved characteristics providing adaptive responses to interferences and exploitation by invasive species, resulting in a high vulnerability. However, there is an intentional or unintentional anthropogenic reversion of the former isolation of island ecosystems. Islands, which have been inhabited by humans, even for short time periods, support a large number of alien species. About 80% of all documented bird and mammal introductions took place on islands (Ebenhard 1998).

Mountain ecosystems are characterized by large environmental gradients, with higher elevations being typically associated with lower temperatures and harsher conditions for plant growth. These include a short duration of the growing season, large snow cover and frequent frost events (Alexander et al. 2009, Pauchard et al. 2009). Variations in many abiotic conditions, such as water availability, temperature, precipitation, and solar radiation may vary largely over small geographical scales along elevation gradients (Alexander et al. 2009). Anthropogenic factors also play an important role in determining patterns in species richness along elevational gradients (e.g. Marini et al. 2009, Pauchard et al. 2009). Elevation gradients are useful because they can be used as proxies for other environmental gradients (both direct and indirect)(Körner 2007).

Increases in stressful abiotic conditions for plant growth, coupled with higher energy constraints, lower propagule pressure and disturbance at high elevations affect native as well as alien species richness, which tend to decline along elevational gradients (e.g. Jentsch and Beierkuhnlein 2003, Marini et al. 2009, Pauchard et al. 2009, Otto et al. 2014). These patterns have been observed in oceanic islands as well as in temperate mountain ecosystems (Marini et al. 2009, Pauchard et al. 2009). It is still not clear if the shape and the strength of the species-energy relationship (e.g. the correlation between the amount of energy received by an assemblage and the number of species that it contains; see Evans et al. 2005) differ between native and alien species (Marini et al. 2009).

Roadways are one of the main anthropogenic features that affect the distribution of native and alien species. Roads are a primary pathway for the spread of alien plants, particularly for generalist species with short life cycles and high reproductive rates (e.g. Pauchard and Alaback 2004), and may interact with elevational gradients facilitating the spread of ring alien species at low and mid-elevations (Pauchard et al. 2009). Because of the disturbance connected with their structure and management, roads represent ideal habitats for the colonization and persistence of alien species, as well as important determinants of their spread (Arévalo et al. 2010). Specifically, roads have a homogenizing effect on resident communities via local extinctions of native species and the spread of alien species with broad environmental ranges (Arévalo et al. 2010). However, there is evidence that endemic species may colonize roadside habitats, particularly those associated with the creation of non-shaded bedrock on steep slopes (Irl et al. 2014a).

Knowledge of the impact of roads on native and alien species along elevation gradients is important to improve our understanding of the potential role of roads in promoting invasions by alien plants (Trombulak and Frissell 2000). In this paper, we examined patterns in species richness for three groups of species, namely endemic, native, and alien species, to improve our understanding of the effects of roads in shaping their diversity patterns, using as a test area the island of Tenerife (Canary Islands, Spain). In the Canary archipelago, the road network has increased dramatically over the past four decades, so that these islands are among the European regions with the highest road density (Arteaga et al. 2009), with paved road occupying 3% of the surface of Tenerife island (Arévalo et al.

2010). There, changes in environmental conditions along elevation gradients represent the major determinant of patterns in plant species communities (Arévalo and Fernandez-Palacios 2005, Whittaker and Fernández-Palacios 2007, Arévalo et al. 2010), consistent with patterns observed for other oceanic islands (Whittaker and Fernández-Palacios 2007). This paper examines the role of different ecological drivers (elevation, road distance, and their interaction) in determining species richness, structuring plant communities at different spatial scales, for endemic, native and alien species. Specifically, we assess: 1) the effect of elevation on endemic, native and alien species richness; 2) the effect of road distance on alien species richness; 3) the effect of elevation and road distance on species richness in endemic, native and alien species.

Methods

Study Site

Patterns in species richness were examined along three roads located in the southern regions of Tenerife. These are single carriage roads going from coastal areas, located approximately 50 km apart from each other, and reaching the same point in the volcanic caldera of Las Cañadas within the Teide National Park (2200-2350 m a.s.l., Fig. 1a). This high-elevation area is connected to the most populated area of the island by the easternmost road and to the less populated area by the westernmost road. In general, these roads are characterized by comparable elevation gradients, construction features (size, material), traffic intensity, and are all south-facing. The three roads converge at Boca de Tauce (Cañadas del Teide National Park) at about 2050 m. Plant communities in the survey area include halophytic communities along the coast, succulent coastal scrub communities in the lowlands, pine forests (between 800-2000 m), and high mountain shrubland above the timber line (Arévalo et al. 2005). Mean annual precipitation ranges from 150 mm to 700 mm (Díaz-Díaz et al. 1999), while mean annual temperature ranges from 22ºC along in coastal areas to approximately 11ºC at the highest elevations. Soils are classified in general as lithosol at lower elevations, pumitic soils and vertic soils between 800-1400 m a.s.l., and cambisols at higher elevation (Rodríguez and Mora 2000).

Data sources

Data have been collected as part of the MIREN project – a Mountain Invasion Research Network – across 6 continents (Pauchard et al. 2009). The sampling design is described in Figure 1b. The length of each road, from sea level to the highest elevation point, was divided into elevation belts of 100 m each. One sampling site was randomly located within each belt, avoiding active agricultural areas and urban settlements. For each road, twenty were thus identified, except for one road, along which only 19 sites were sampled due to the presence of human settlements. At each site, a T-transect consisting of 15 plots (2 m x 10 m each) was sampled (Figure 1b). Five plots (plots 1-5) were located on the edge of the road, with their long side parallel to the road itself. Ten additional plots (plots 6-15) were located with their long side perpendicular to the road, departing from it at plot 3. Each transect was divided into three sections, one parallel to the road (*road*: plots 1-5, section 1), and two perpendicular to the road. These were divided into: i) *close plots* (plots 6-10, section 2), *i.e.* the five perpendicular plots closer to the road, and ii) *far plots* (plots 11-15, section 3). A total of 885 plots was sampled.

Plant species richness and composition were recorded in each plot, including juveniles and seedlings. Field sampling was performed in 2008 in January-March. Species nomenclature and origin status (*endemic*: native of Tenerife and endemic of Canary Islands; *native*: native to Tenerife but more largely distributed beyond the Canarian archipelago; or *alien*: non-native species) follow Izquierdo et al. (2004). Species were classified into three groups based on their status: native of Tenerife and endemic of Canary Islands (hereafter called *endemic*), native to Tenerife but more largely distributed beyond the Canarian archipelago (*native*) and introduced to Tenerife (*alien*) - follow Izquierdo et al. (2004). Most of the alien species recorded in Tenerife are of Mediterranean origin (Arteaga et al. 2009), and their introduction is probably related to the long history of human activity and landscape transformation at mid-elevation areas that has occurred since the prehistoric times. The pooled species richness for the three groups is referred to as the *all species* group.

Data analysis

Gradient Analysis

As a first explorative analysis, the number of species observed at transect scale was plotted against elevation for each group (endemic, native and alien species) and for *all species*. Each species group was fitted to the linear and 2nd order polynomial transformation of the elevation by using Poisson regression models, using the log-link function (McCullagh and Nelder 1989, for an application focused on islands; see also Chiarucci et al. 2011). The best descriptive model (linear vs. polynomial) was determined, by computing the adjusted D^2 statistics (similar to the adjusted coefficient of determination, see Bacaro et al. 2008, Gioria et al. 2010) for each model, and then comparing the amount of residual deviance between the two models (likelihood ratio test).

Secondly, a univariate permutational analysis of variance (Anderson 2001) based on the Euclidean distance of the log-transformed (log x+1) mean number of species per each *Section* was applied, to test the effects of three predictor variables on all, endemic, native, and alien species richness: *Road* (fixed, three levels), *Transect* (random, nested within *Road*), and *Section* (fixed, three levels: *road*, *close* and *far*; crossed with *Road* and *Transect*). A posteriori pair-wise comparisons were applied when analysis of variance resulted significant for the factors *Section* and *Road x Section*. Analyses were performed using the PERMANOVA routine, in the PRIMER v6 computer program (Clarke and Gorley 2006), including the add-on package PERMANOVA+ (Anderson et al. 2008). All tests were performed with 9999 permutations of residuals under a reduced model using Type III sums of squares.

Spatial components of plant diversity

Alpha, beta and gamma diversity were calculated at different spatial scales (plot, section, transect, road and whole sample) for each plant group (endemic, native and alien) and for *all species*. Mean values were expressed as the proportion of mean species richness at each spatial scale. The contribution of each spatial component (plot, section, transect and road) to the total species diversity was quantified using additive partitioning of species richness (Gering et al. 2003). By following this approach, *inventory diversity* is the α diversity, i.e. the number of species found in a given unit (plot, section, transect, road or whole sample =

island), while *differentiation diversity* (β diversity, turnover) is the mean number of species of the upper level that are, on average, absent from the sampling units of the given level. Total diversity of the whole sampling area is an inventory diversity that corresponds to the classical γ diversity (sensu Whittaker 1972). Species richness in the whole sampling area (island) was partitioned into the inventory diversities at the various spatial scales (αPlot, αSection, αTransect, αRoad), that summed to the differentiation diversities for the corresponding spatial scales (βPlot , βSection , βTransects , βRoads) to give the total diversity of the whole sampling area (γ) (see Crist and Veech 2006 for a graphical representation of the adopted partition scheme, please refers to Figure 1 in Chiarucci et al. 2008). In a hierarchical sampling design with i = 1, 2, 3, ..., m levels of sampling with samples in lower hierarchical levels nested within higher level units from i=1 to i=m grain size, the α_i component of diversity can be defined as the average diversity found within samples. At the highest sampling level, the diversity components are calculated as:

(1) $\beta_m = \gamma - \alpha_m$

while for each lower sampling level as

(2) $\beta_i = \alpha_{(i+1)} - \alpha_i$

Then, the additive partition of diversity is

(3). $$\gamma = \alpha_i + \sum_{j=i}^{m} \beta_j$$

The software PARTITION 2.0 (Veech and Crist 2007a, b) was used to test for departure from random expectations of species richness values for each of the three groups and for *all species*, at each hierarchical level, using a sample based randomization test (see Veech and Crist 2007a,b). For each level, a null statistical distribution model of expected values was created by using 10,000 iterations of the randomization routine. The randomization procedure consisted in the random allocation of lower-level samples among higher-level samples. The statistical significance of each diversity component was assessed as the proportion of null values greater than (or less than) the observed diversity value. This proportion was expressed by a *P*-value, indicative of the probability of obtaining a diversity

value greater (or smaller) than the observed one by chance. Because this randomization procedure was based on the permutations of the samples at the lowest level (plots), the null expected values at the plot level could not be calculated. As suggested by Schmera and Podani (2013) additive partitioning is only one of the possible methods to estimate the contribution of different levels of sampling hierarchy to landscape diversity. We are aware that additive partitioning is not free from disadvantages. The main drawback in the additive decomposition method across spatial scales is that α and β diversity are not independent (Jost 2007). However, the direct interpretation of the additive method makes it particularly useful and widely used for descriptive purposes. For future analyses, more promising approaches would consider pairwise dissimilarities and they are based on partitioning the dissimilarity matrix of sampling units (Bacaro et al. 2012, 2013, Schmera and Podani 2013).

RESULTS

Species richness and elevation

Vascular plant species were recorded in 784 in 885 sampled plots (88.6%), while no species were found in the remaining 101 plots. In total, 244 plant species were recorded along the three roads, of which 62 endemic species (25.4%) and 148 native to Tenerife (60.7%). The species recorded in more than 5% of the transects, together with their elevation range, are listed in Appendix I. The most frequent endemic and native species recorded in the study plots were *Pinus canariensis* (24.5% of the plots), *Argyranthemum frutescens* (18.0%), *Kleinia neriifolia* (17.7%), *Forsskaolea angustifolia* (15.0%), *Bituminaria bituminosa* (14.1%), *Hyparrhenia hirta* (13.7%), *Euphorbia lamarckii* (13.6%), *Micromeria hyssopifolia* (12.8%), *Pterocephalus lasiospermus* (11.8%) and *Wahlembergia lobelioides* (10.1%). All these species but *B. bituminosa*, *H. hirta*, and *W. lobelioides* are endemic to Canary Islands.

Alien species represented the remaining 13.9% of the recorded flora (34 species). The most frequent species at the plot scale were *Opuntia ficus-indica* (9.7%), *Conyza bonariensis* (4.2%), *Mesembryanthemum nodiflorum* (3.1%), *Eschscholzia californica* (2.8%),

Mesembryanthemum crystallinum (2.8%), *Opuntia dillenii* (1.9%), *Pennisetum setaceum* (1.8%), *Nicotiana glauca* (1.7%), *Atriplex semibaccata* (1.2%), *Digitaria sanguinalis* (1.1%) and *Vitis vinifera* (1,1%). One of the alien species, *Asteriscus sericeus*, is endemic to Fuerteventura, Canary Islands, but, since it was planted along roads in Tenerife, it is considered here an alien species.

The number of species per plot ranged from 0-12 for *endemic* species, 0-21 for *native* species, and 0-5 for *alien* species. Species richness for *all species* ranged from 0-23 (average 5.97). Distribution of species richness values per plot was highly skewed, with a prevalence of low values of species richness.

Regression models showed a unimodal pattern of species richness in relation to elevation, although marked differences between the three groups of plants with different origin status were evident (Table 1). Species richness for *all species* increased with elevation up to 650 m a.s.l., while decreased at higher elevations (the maximum predicted value by the regression model was reached at 648 m a.s.l., Figure 2a). Endemic species showed a similar pattern, although they peaked at a lower elevation (the maximum predicted value was reached at 627 m a.s.l.), and showed a less steep decrease at higher elevations (Figure 2b). *Native* species richness followed a pattern similar to *all species*, although a more steep decrease with increasing elevations was recorded (expected maximum at 708 m a.s.l., Figure 2c). A different pattern was recorded for *alien* species, with an expected maximum at 370 m a.s.l. (up to four species per plot), and a progressive decrease with elevation (less than 1 alien species is expected to be found above the 1267 m a.s.l. threshold, see Figure 2d). Similar patterns of species richness in relation to elevation were observed at the plot scale for all four groups of species (data not shown).

PERMANOVA analyses showed that factor *Road* had no significant effect on species richness (Table 2), while factor *Transect* within road was significant for endemic, native and alien species. Interestingly, the factor *Section*, representing distance from road, did not show any significant effect on species richness for *native* and *all species* at the plot scale. Conversely, the number of *alien species* decreased from *section road* to *section far* (Table 2; mean *road* plots = 0.5; mean *far* plots = 0.33). Post-hoc tests showed that differences in species richness were significant only between *sections road* and *far* ($t = 2.278$, $P = 0.03$)

and between *road* and *close* (t = 2.16, P = 0.03). The number of endemic species showed a different pattern, being higher for the *section close* (2.65), and decreasing in the *far section* (2.34) and in the *road* section (2.23). *Post-hoc* tests showed that differences in species richness for endemic species were significant only between the *road* and *close* sections (t = 2.51, P = 0.014) and between the *close* and *far* sections (t = 2.22, P = 0.03). Finally, the investigated interaction (*Road* x *Section*, Figure 3) resulted significant for native and alien species: the testing of *Road* x *Section* interaction showed that, on average, the distribution of the total number of plant species (*all species*) and the number of endemic species did not differ from road to road, and did not depend on the distance of sampled plots from the road edge (Table 2). However, the distribution of *native* and *alien* species, if related to road edges, was found to depend to the factor *Road*. In particular *Post-hoc* tests showed that differences in species richness for alien species were significant between the *road* and *close* sections (t = 3.02, P = 0.01) and between the *road* and *far* sections (t = 3.19, P = 0.005) within level 2 of factor Road only. Species richness for *native* species was significant for the *road* and *close* sections (t = 2.53, P = 0.014) for Road 2 only.

Hence, the presence of endemic and native versus alien species differed in transects sampled at different elevations. The diversity of alien species was clearly determined by distance to the road edge, with *far* (e.g. remote) plots representing the native vegetation, harboring significantly less alien species than roadside communities.

Spatial patterns of species richness

The proportion of endemic species over the total number of species decreased at coarser spatial scale, while the proportion of native and alien species increased (Table 3). In particular, alien species richness doubled its relative importance from the finest (plot) to the coarsest (flora of the study area) spatial scale.

The partitioning of species richness into the three groups showed that species complementarity (i.e., the mean number of species not shared among plots) observed at the *section* scale was higher than that expected from the null models for the three groups of plants with different origin status (Figure 4). Thus, significant compositional differences

existed between the three different sections of each transect, and once the plots were permuted this resulted in significantly higher species richness.

The two coarser spatial scales, transect and road, accounted for a higher proportion of species richness for each plant group. The third level of β-diversity (across transects within the same road) was significantly higher than that expected for the three groups, due to the large elevation gradient existing along each road, ranging from nearly sea level to more than 2000 m a.s.l.). The fourth β component (across different roads) was not significantly different from the null expectation for both the endemic and native species. This indicates that these two groups had basically the same species composition in the three roads, and thus did not display any compositional complementarity. On the contrary, *alien* species showed significant β diversity across the three roads, indicating that species composition of alien species differed across each road, with each road having different alien species.

Discussion

The role of elevation and human impact on the distribution of plant species richness

Elevation and human disturbance, such as the presence of roads, may strongly affect the distribution of native and alien species (Pauchard and Alaback 2004, Marini et al. 2009, Pauchard et al. 2009, Marini et al. 2013, Irl et al. 2014b). Assessing patterns of plant species richness along roads and elevation gradients can provide important insights into the effects of anthropogenic disturbances on plant communities, especially as far as island and mountain ecosystems are concerned. The peak in species richness was observed at intermediate elevation for both native and endemic species. This is likely due to the correlation of the elevation gradient with other environmental gradients, which are known to drive the distribution of plants (e.g. Fernandez-Palacios 1992, Arteaga et al. 2009). In particular, variables such as high humidity (derived from mean annual precipitation plus trade wind interception), low thermal stress, and high productivity tend to reach a maximum at intermediate elevations in the Canary Islands (Arévalo et al. 2005). Drought stress characterizing both low (sea level) and high elevations, and low temperatures at high elevation represent major environmental filters to the establishment of a species (Irl et al.

2014b). Thus, plant communities occurring at low or high elevations may support less species than those at intermediate elevations. A peak of alien species richness (at the scale of transect) was observed within 100-600 m a.s.l. elevation range, with a tendency for a decreasing non linear-relationship with increasing elevation. Above 600 m a.s.l., the number of alien species decreased progressively to zero. This is consistent with the results of previous investigations in continental mountain systems (Pauchard and Alaback 2004, Siniscalco et al. 2011, Barni et al. 2012, see Pauchard et al. 2009 and references therein). In oceanic islands a unimodal distribution pattern along the elevation gradient was also described (Arévalo et al. 2005; Jackobs et al. 2010), with a relatively high number of alien species even at high altitudes, especially in connection to human activities (Kitayama and Mueller-Dombois 1995).

Climatic conditions are considered the main constraints to the spread of alien species along elevation gradients. For instance, Marini et al. (2009), testing the relationships between native and alien richness with a range of environmental predictors along the elevation gradient in the eastern Alps, showed that the distribution of alien plant species was mainly determined by mean annual temperature (40% of variance explained), and to a lesser extent, by human population density. However, other authors (e.g. Nogues-Bravo et al. 2008) pointed out that, on average, human land use is concentrated at low elevations, increasing the opportunities for the introduction and establishment of propagules, consistent with our results, which showed a peak of alien species richness at a relatively low elevation. Following Marini et al. (2013) the observed peak of alien species richness at low elevation might be related to human intervention. Strictly speaking, humans might have introduced species in the lowlands at different points in space and in time, through multiple pathways and often in a haphazard fashion.

Our results confirm the important role of elevation, summarizing information on a range of climatic and abiotic variables, land use and human disturbance as a major determinant of patterns in species richness for endemic, native, and alien species. Specifically, we observed that transect differences, namely species complementarity occurring at the higher sampling spatial scale, account for most of the observed variability in the distribution of species richness values. This pattern was expected because distribution of transects was

strongly correlated with elevation. More in general, the high significance of the factor transect in PERMANOVA tests is a clear indication of the climatic variation throughout the considered elevation. Moreover, other environmental factors play a central role in shaping the distributional pattern of endemic, native and alien species.

Generally, roadsides are characterized by environmental conditions and disturbances that differ substantially from those found in the habitats in their proximity (Trombulak and Frissell 2000), thus resulting in road-specific plant communities. In steep mountain areas and on high-elevation oceanic islands, where roads are cut into slopes, these environmental factors could have a high relevance (Irl.et al. 2014b). Besides influencing the environmental conditions in their proximity, the impact of roads on plant communities typically varies with the distance from the road edge (Spellerberg 1998).

In our study, roads and distance from the road edge played a major role in determining patterns of plant species richness. *Post-hoc* tests clearly highlighted this pattern, showing that alien species tend to remain confined on the road edge, and their number is significantly higher than that found in plots located at intermediate and far distances from roads in resident communities, consistent with previous findings. This was expected, as roads may facilitate the dispersal of propagules of alien species via three main mechanisms: 1) roads are a source of disturbance and create new environmental conditions that are suitable to ruderal and pioneer species, 2) they facilitate the dispersal of propagules via air movement associated with the transit of vehicles, and 3) they may facilitate colonization by alien species by suppressing the growth or removing stands of native species (Trombulak and Frissel 2000). The differences in the number of alien species close to and far from roads suggest the importance of all these mechanisms in facilitating the spread of alien species, while less disturbed areas (away from roads) tend to be more resistant to the colonization by alien species.

Native species in resident communities far from the road carry traits that do not allow invasive species to enter the community without disturbance (e.g., native may fill all spatial and temporal niches avoiding alien species to colonize without any disturbance). However, our results also suggest that the three investigated roads have different patterns of alien species invasion, likely due to the different features of the connected sites and their level of alien invasion.

Spatial components of plant diversity

Additive partitioning of species richness showed that the highest contribution to total diversity (γ-diversity) was largely due to the β component of diversity, which reflects compositional differences across sites at larger spatial scales (e.g. Crist and Veech 2006, Chiarucci et al. 2010). This was in our study represented by three roads along an elevation gradient from sea level to mountain top. The overall diversity for all species groups was mainly associated with the larger-scale components of β-diversity (in particular βTransect and βRoad), including endemic and native species. For these groups, the highest contribution to total diversity was given by the species complementarity (i.e. differences in species composition) between transect within each road (βTransects), indicative that elevation is the most important determinant of species richness for native and endemic species on Tenerife Island.

These patterns are probably associated with the evolutionary history of endemic and native species, which have adapted to those specific local conditions occurring along elevation (and climatic) gradients. For instance, Marini et al. (2013) pointed out a weaker nested pattern for native species, indicating a larger species niche differentiation between lowlands and high mountains. In other words, lowlands and high-elevation areas share a small percentage of native species while a large number of species are exclusively present at low or the high elevation areas only.

In contrast, βRoads summarizing the effects of disturbance created by the three roads is the most important diversity component for *alien* species, indicative of the major role of roads (in terms of road identity) in determining the species richness and composition of alien species, possibly reflecting road-specific conditions such as the disturbance regime. This is consistent with the results of a study investigating invasion by alien species along two mountain roads located in two different regions, showing that anthropogenic disturbance may be more important than climate in determining successful invasions (Alexander et al. 2009). Marini et al. (2013) observed a similar pattern in beta diversity of alien species in two mountain areas in Italy and showed that species replacement did not occur along the elevation gradient, but mostly within the same elevation belts. Similarly, in our study we can assume that the higher βRoads values are the result of the spatial distribution of the

introduction routes in the area, where different locations are physically connected to lowland areas by the network of streets and urban settlements. On the other side, dispersal between high-elevation and different faced slopes of the island are expected to be less likely associated with impervious physical barriers and climatic constrains (Becker et al. 2005).

Alien species were absent from plots located at high elevation, consistent with previous observations (Pauchard and Alaback 2004), suggesting that i) the observed decline of alien species richness with elevation is probably due to the lack of introduction of alien species adapted to grow at high elevations (McDougall et al. 2005, Alexander et al. 2009, Alexander and Edwards 2010, Siniscalco et al. 2011), and ii) niche boundaries provide the fundamental constraints for the spread of alien species (Alexander et al. 2009). These results confirm the predictions of the directional ecological filtering hypothesis that have been used to explain invasions of alien species in mountain regions. The aliens are introduced at low elevations and spread upwards from there, and the alien species occurring at higher elevations are composed of nested subsets of the lowland communities (Marini et al. 2013).

Conclusion

To our knowledge, this study is the first attempt to use the additive partitioning of species diversity (as proposed by Lande 1996, Wagner et al. 2000, Bacaro and Ricotta 2007) to compare the different components of plant diversity for plant groups of different origin (endemic, native and alien species). We found that the variation in species richness for different species groups was not equally accounted for by coarse scale differences and elevation. Specifically, assembly of alien plant communities differed from that of native and endemic species, being primarily driven by processes occurring where human pressure is the highest (lowlands and close to road edges) and only secondarily by the climate filtering along the elevational gradients. Improving our knowledge of how elevation gradients, reflecting climatic as well as anthropogenic disturbances, and direct disturbances

such as those caused by roads, during and after their construction, will provide important insights into the mechanisms and processes underlying successful invasions in islands and/or mountain regions. Future investigations on this topic would greatly benefit from a classification of alien species into invasive, naturalized, and casual species (Richardson and Pyšek 2012), as it would allow identifying those species that are facilitate by the disturbance regime associated with roads and that can cope with broad environmental conditions (naturalized and invasive species) from those that, despite being introduced and spread even at considerable distances from roads cannot cope with the environmental conditions associated with high elevations. Detailed analyses including life history traits would also reveal which functional groups is more likely to cause a large impact on the diversity of endemic and native plant species. Specific hypothesis on the causes of the spread of invasive species in resident communities along distance gradients perpendicular to roads deserves further explorations.

Acknowledgements

References

Alexander, J.M., Naylor, B., Poll, M., Edwars, P.J. and Dietz, H. 2009. Plant invasions along mountain roads: the altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges. *Ecography.* 32: 334–344.

Alexander, J.M. and Edwards, P.J. 2010. Limits to the niche and range margins of alien species. *Oikos.* 119: 1377–1386.

Anderson, M.J. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences.* 58: 626–639.

Anderson, M.J., Gorley, R.N. and Clarke KR. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth, UK.

Arévalo, J.R., Otto, R., Escudero, C., Fernández-Lugo, S., Arteaga, M., Delgado, J. and Fernández-Palacios, J.M. 2010. Do anthropogenic corridors homogenize plant communities at a local scale? A case studied in Tenerife (Canary Islands). *Plant Ecology.* 209: 23–25.

Arévalo, J.R. and Fernandez-Palacios, J.M. 2005. Gradient analysis of exotic *Pinus radiata* plantations and potential restoration of natural vegetation in Tenerife, Canary Islands (Spain). *Acta Oecologica.* 27: 1-8.

Arteaga, M.A., Delgado, J.D., Otto, R., Fernandez-Palacios, J.M. and Arévalo, J.R. 2009. How do alien plants distribute along roads on oceanic islands? A case study in Tenerife, Canary Islands. *Biological Invasions.* 11: 1071–1086.

Bacaro, G. and Ricotta, C. 2007. A spatially explicit measure of beta-diversity. *Community Ecology.* 8: 41–46.

Bacaro, G., Rocchini, D., Bonini, I., Marignani, M., Maccherini, S. and Chiarucci A. 2008. The role of regional and local scale predictors for plant species richness in Mediterranean forests. *Plant Biosystems.* 142: 630–642.

Bacaro, G., Gioria, M. and Ricotta, C. 2012. Testing for difference in beta diversity from plot-to-plot dissimilarities. *Ecological Research.* 27: 285–292.

Bacaro, G., Gioria, M. and Ricotta, C. 2013. Beta diversity reconsidered. *Ecological Research.* 28: 537–540.

Barni, E., Bacaro, G., Falzolai, S., Spanna, F. and Siniscalco, C. 2012. Establishing climatic constraints shaping the distribution of alien plant species along the elevation gradient in the Alps. *Plant Ecology.* 213: 757–767.

Becker, T., Dietz, H., Billeter, R., Buschmann, H. and Edwards, P.J. 2005. Altitudinal distribution of alien plant species in the Swiss Alps. *Perspectives in Plant Ecology, Evolution and Systematics.*7: 173-183.

Chiarucci, A., Bacaro, G., Arévalo, J.R., Delgado, J.D. and Fernandez-Palacios, J.M. 2010. Additive partitioning as a tool for investigating the flora diversity in oceanic archipelagos. *Perspectives in Plant Ecology, Evolution and Systematics*. 12: 83–91.

Chiarucci, A., Bacaro, G. and Rocchini, D. 2008. Quantifying plant species diversity in a Natura 2000 network: Old ideas and new proposals. *Biological Conservation*. 141: 2608-

2618.

Chiarucci, A., Bacaro, G., Triantis, A.K. and Fernandez-Palacios, J.M. 2011. Biogeographical determinants of pteridiophytes and spermatophytes on oceanic archipelagos. *Systematics and Biodiversity.* 9: 191–201.

Clarke, K.R. and Gorley, R.N. 2006. PRIMER V6: user manual/tutorial. PRIMER-E Ltd, Plymouth, UK.

Courchamp, F., Chapuis, J.L., Pascal, M. 2003. Mammal invaders on islands: impact, control and control impact. *Biological Reviews.* 78: 347–383.

Crist, T.O. and Veech, J.A. 2006. Additive partitioning of rarefaction curves and species-area relationships: unifying alpha-, beta- and gamma-diversity with sample size and habitat area. *Ecology Letters.* 9: 923–932.

Díaz-Díaz, R., Loague, K. and Notario, J.S. 1999. An assessment of agrochemical leaching potentials for Tenerife. *Journal of Contaminant Hydrology.* 36: 1–30.

Ebenhard, T. 1988. Introduced birds and mammals and their ecological effects. *Swedish Wildlife Research.* 13: 1–107.

Evans, K.L., Warren, P.H. and Gaston, K.J. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews.* 80: 1–25.

Fernandez-Palacios, J.M. 1992. Climatic response of plant species on Tenerife (Canary Island). *Journal of Vegetation Science.* 3: 595–602.

Gering, J.C., Crist, T.O. and Veech J.A. 2003. Additive Partitioning of Species Diversity across Multiple Spatial Scales: Implications for Regional Conservation of Biodiversity. *Conservation Biology.* 17: 488–499.

Gioria, M., Bacaro, G. and Feehan, J. 2010. Identifying the drivers of pond biodiversity: the agony of model selection. *Community Ecology.* 11: 179–186.

Irl, S.D.H., Steinbauer, M.J., Epperlein, L., Harter, D., Jentsch, A., Pätz, S., Wohlfart, C.H. and Beierkuhnlein, C. 2014b. The hitchhiker's guide to endemism - biodiversity and endemic species in 4 roadside and natural island vegetation. *Biodiversity and Conservation.* 23: 2273–2287.

Izquierdo, I., Martín, J.L., Zurita, N. and Arechavaleta, M. 2004. Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias. Santa Cruz de Tenerife, Santa Cruz de Tenerife, Spain.

Jakobs, G., Kueffer, C. and Daehler, C.C. 2010. Introduced weed richness across altitudinal gradients in Hawai'i: humps, humans and water-energy dynamics. *Biological Invasions.* 12: 4019–4031.

Jentsch, A. and Beierkuhnlein, C. 2003. Global climate change and local disturbance regimes as interacting drivers for shifting altitudinal vegetation patterns in high mountains. *Erdkunde.* 57: 216-231.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology.* 88: 2427-2439.

Kitayama, K. and Mueller-Dombois, D. 1995. Biological invasion on an oceanic island mountain: Do alien plant species have wider ecological ranges than native species? *Journal of Vegetation Science.* 6: 667–674.

Körner, C. 2007. The use of "altitude" in ecological research. *Trends in Ecology and Evolution.* 22: 569-574.

Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos.* 76: 5–13.

Marini, L., Gaston, K.J., Prosser, F. and Hulme, P.E. 2009. Contrasting response of native and alien plant species richness to environmental energy and human impact along alpine elevation gradients. *Global Ecology and Biogeography.* 18: 652–661.

Marini, L., Bertolli, A., Bona, E., Federici, G., Martini, F., Prosser, F. and Bommarco, R. 2013. Beta-diversity patterns elucidate mechanisms of alien plant invasion in mountains. *Global Ecology and Biogeography.* 22: 450–460.

. and Nelder, J.A. 1989. Generalized Linear Models, Second Edition. Boca McCullagh, P Raton: Chapman and Hall/CRC.

McDougall, K.L., Morgan, J.W., Walsh, N.G. and Williams, R.J. 2005. Plant invasions in treeless vegetation of the Australian Alps. *Perspectives in Plant Ecology, Evolution and Systematics.* 7: 159–171.

Nogués-Bravo, D., Araújo, M.B., Romdal, T. and Rahbek, C. 2008. Scale effects and human impact on the elevational species richness gradients. *Nature.* 453: 216–220.

Otto, R., Arteaga, M.A., Delgado, J.D., Arévalo, J.R., Blandino, C. and Fernandéz-Palacios, J.M. 2014. Road edge effect and elevation pattern of native and alien plants on an oceanic island (Tenerife, Canary Island). *Folia Geobotanica.* 49: 65–82.

Pauchard, A. and Alaback, P.B. 2004. Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. *Conservation Biology.* 18: 238-248.

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C.C., Alexander, J., Edwards, P.J., Arevalo, J.R., Cavieres, L.A., Guisan, A., Haider, S., Jakobs, G., McDougall, K., Millar, C.I., Naylor, B.J., Parks, C.G., Rew, L.J. and Seipel, T. 2009. Ain't no mountain high enough: plant invasions reaching new elevations. *Frontiers in Ecology and the Environment.* 7: 479-486.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M. and Kirschner, J. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53:131–143.

Richardson, D.M. and Pyšek, P. 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytologist*. 196: 383–396.

Rodríguez, A. and Mora, J.L. 2000. Los suelos. In G. Morales and R. Pérez (eds). *Gran

atlas temático de Canarias. Interinsular Canaria. S/C de Tenerife. pp. 107-120.

Schmera, D., Podani, J. 2013. Components of beta diversity in hierarchical sampling designs: A new approach. *Ecological Indicators.* 26: 126–136.

Siniscalco, C., Barni, E. and Bacaro, G. 2011. Non-native species distribution along the elevation gradient in the western Italian Alps. *Plant Biosystems.* 145: 150–158.

Spellerberg, I.F. 1998. Ecological effects of roads and traffic: a literature review. *Global Ecology and Biogeography Letters.* 7: 317–333.

Steinbauer, M. J., Irl, S. D. and Beierkuhnlein, C. 2013. Elevation-driven ecological isolation promotes diversification on Mediterranean islands. Acta Oecologica. 47: 52-56.

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

Veech, J.A. and Crist, T.O. 2007a. PARTITION: software for hierarchical additive partitioning of species diversity, version 2.0.

Veech, J.A. and Crist, T.O. 2007b. Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. *Global Ecology and Biogeography.* 16: 650–656.

Wagner, H.H., Wildi, O. and Ewald, K.C. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology.* 15: 219–227.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon.* 21: 213–251.

Whittaker, R.J. and Fernández-Palacios, J.M. 2007. Island Biogeography. Ecology, Evolution and Conservation. Oxford University Press, New York.

TABLE CAPTIONS

Table 1. Summary statistics comparing the fitted linear and polynomial relationship between elevation and the three species groups and for all the species at the transect scale. All the results are based on Poisson models with the "log" link function. Tests for the likelihood ratio tests are based on the X^2 distribution; *** $p < 0.001$, ** $p < 0.01$, *$p < 0.05$.

Table 2. Results of the Univariate Permutational Analysis of Variance (PERMANOVA) based on the Euclidean distance calculated on all species, endemic, native and alien species richness.

Table 3. Mean number and proportion (as %) of the three groups of species (endemic, native and alien) at the five different spatial scales used for this investigation.

Table 1

	Model Fitting	Coefficients values and signs	D^2_{adj}	Likelihood ratio test Linear vs. Polynomial Fit (X^2 test)
All species	Linear	-0.001***	0.461	<2.2e-16
	Polynomial	-5.237***, -2.988***	0.690	
Endemic species	Linear	-0.001***	0.219	0.0016
	Polynomial	-2.235***, -1.224**	0.287	
Native species	Linear	-0.001***,	0.376	<2.2e-16
	Polynomial	-7.252***, -4.701***	0.677	
Alien species	Linear	-0.001***	0.543	1.113e-05
	Polynomial	-14.470***, -5.300***	0.654	

Table 2

Source of Variation	df	All Species			Endemic		
		MS	F	P	MS	F	P
Road	2	1.0621	0.64428	0.5216	0.1942	0.0278	0.9733
Transect (Road)	56	1.6484	17.032	**0.0001**	6.9964	9.9536	**0.0001**
Section	2	0.0661	0.68257	0.5129	2.816	4.0061	**0.0197**
Road × Section	4	0.1573	1.625	0.1688	1.5222	2.1656	0.0799
Residual	112	0.0968			0.7029		
Total	176						

Source of Variation	df	Native			Alien		
		MS	F	P	MS	F	P
Road	2	0.3626	0.1796	0.8274	0.0586	0.1785	0.8407
Transect (Road)	56	2.0191	22.21	**0.0001**	0.3285	8.7473	**0.0001**
Section	2	0.0854	0.9395	0.4005	0.1474	3.9259	**0.0221**
Road × Section	4	0.3180	3.4988	**0.0081**	0.1583	4.214	**0.0035**
Residual	112	0.0909			0.0376		
Total	176						

Table 3

Group		Spatial Scale				
		Plot	Section	Transect	Road	Whole Sample
Endemic	N	2.4	4.7	7.2	39.0	62.0
	%	40.3	36.2	32.2	27.0	25.4
Native	N	3.2	7.3	13.3	87.7	148.0
	%	53.0	56.7	59.6	60.7	60.7
Alien	N	0.4	0.9	1.8	17.7	34.0
	%	6.6	7.1	8.3	12.2	13.9

FIGURE CAPTIONS

Figure 1. Location of the three sampled roads in the southern part of Tenerife, Canary Islands (upper section of the figure) and representation of the arrangement of the 15 plots in the T-transect located on the side of each sampling point along the roads (lower part of the figure): the road and the plots are represented in a schematic way, not to scale. The first five plots are locate in a transect parallel to the road (1 to 5), while the remaining ten plots are perpendicular to the road from the center of the transect from the plots 1 to 5. All the plots are rectangular (1 x 2 m).

Figure 2. Species richness patterns at the whole transect scale, in relation to the elevation for the four groups of plants considered in the analyses. Continuous lines represent the best descriptive model relating elevation to each species group.

Figure 3. Analysis of the Road X Sector interaction for the four group of plants analysed by univariate permutational analysis of variance. Significant interactions occurred for endemic, native, and alien species (see Table 2).

Figure 4. Percentage of total plant species richness explained for each of the three groups by alpha (plot scale) and the beta components of diversity on four spatial scales: plot, section, transect and road. The contributions to the total richness for each scale were determined by the additive partitioning of diversity (+++ = the diversity value is statistically higher than the observed at $p < 0.001$; --- = the diversity value is statistically lower than the observed at $p < 0.001$, NS= Not Significant).
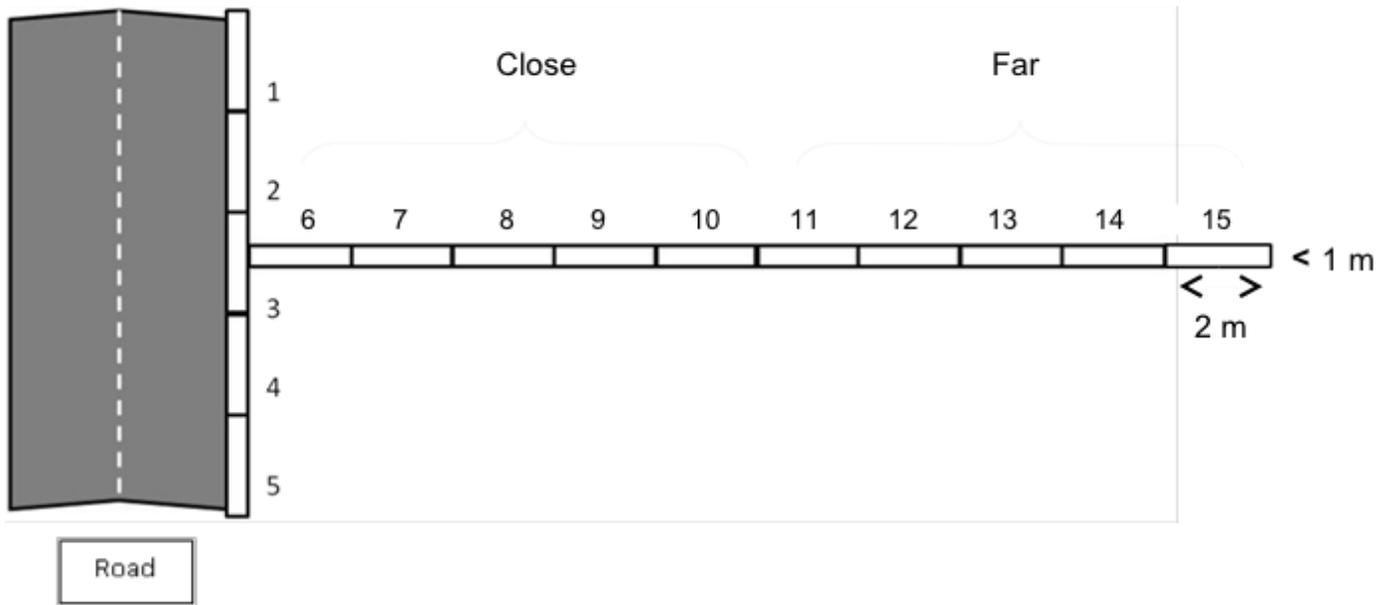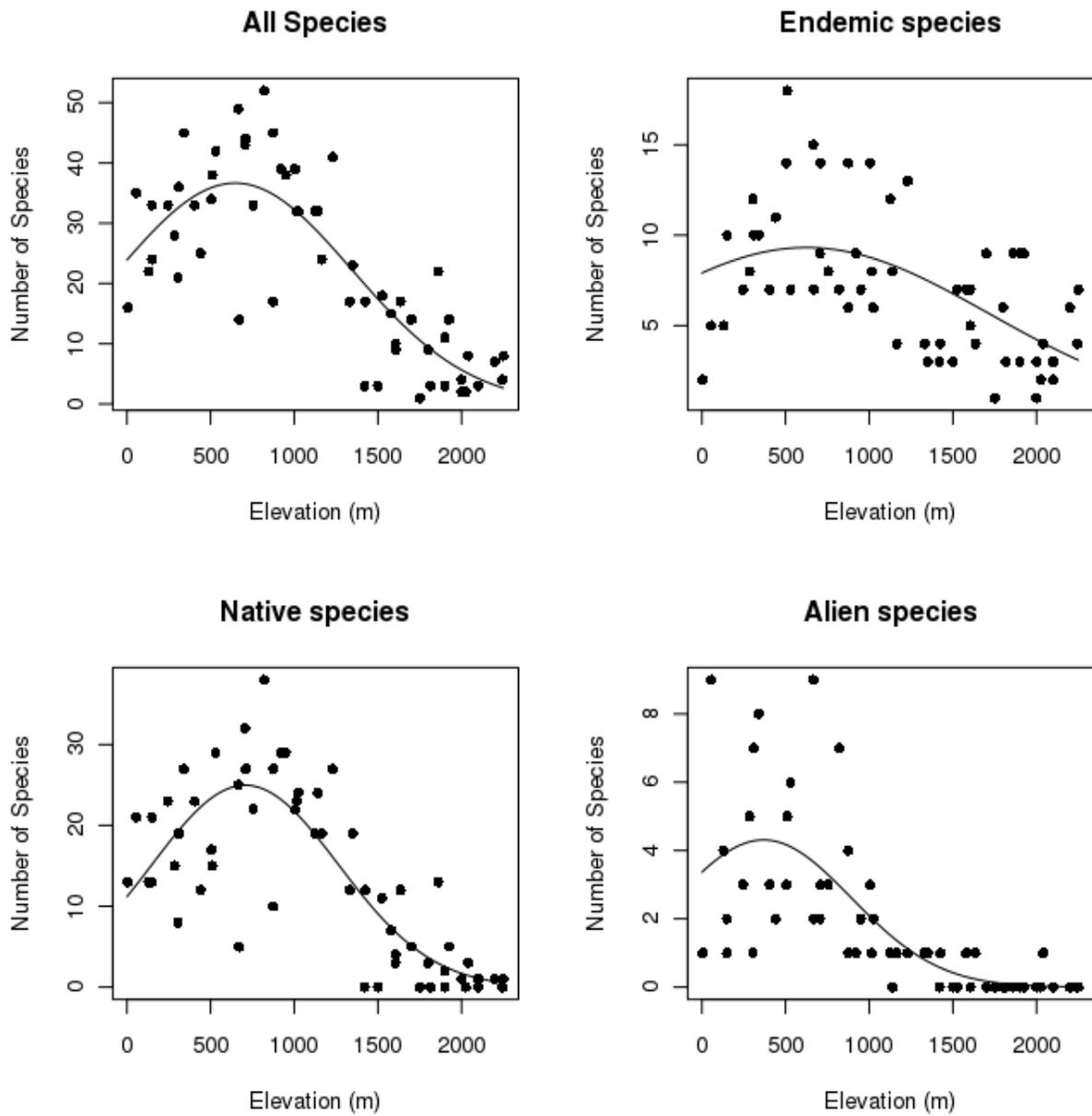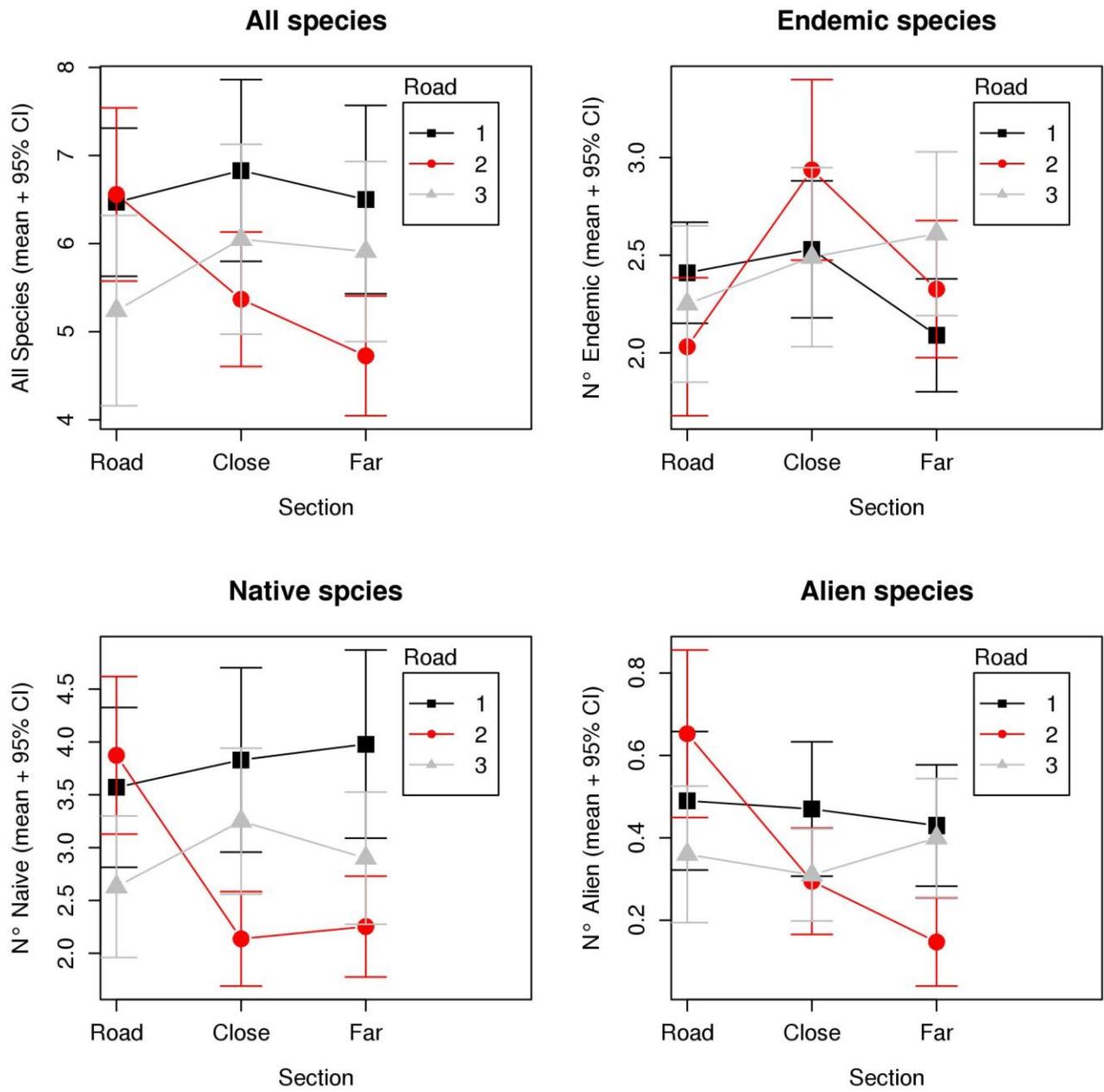
Figure 1

Tenerife Island

Figure 2

Figure 3

Figure 4