



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

G. Bacaro^{1,9}, S. Maccherini², A. Chiarucci³, A. Jentsch⁴, D. Rocchini⁵, D. Torri⁶,
M. Gioria⁷, E. Tordoni¹, S. Martellos¹, A. Altobelli¹, R. Otto⁸, C. G. Escudero⁸,
S. Fernández-Lugo⁸, J. M. Fernández-Palacios⁸ and J. R. Arévalo⁸

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

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

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

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

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

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

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

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

⁹Corresponding author. E-mail: giofbac@gmail.com

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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. Although evidence shows that corridors may facilitate plant invasions, the question of 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 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 × 2 m, along three major roads each placed over 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 richness were also affected by elevation, with a decline in richness with increasing elevation and no alien species 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 the richness of alien species (which are not adapted to high elevations), while anthropogenic pressures may explain the richness of alien species at low elevation.

Nomenclature: Izquierdo et al. (2014)

Abbreviations: MIREN—Mountain Invasion Research Network; PERMANOVA—Permutational Analysis of Variance.

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. In contrast, less

attention has been 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 competition by invasive species, resulting in a high vulnerability. Moreover, 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).

Roads 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. 2015).

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

Materials and 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 22°C along in coastal areas to approximately 11°C 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 six 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 × 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 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) - following 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.

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)

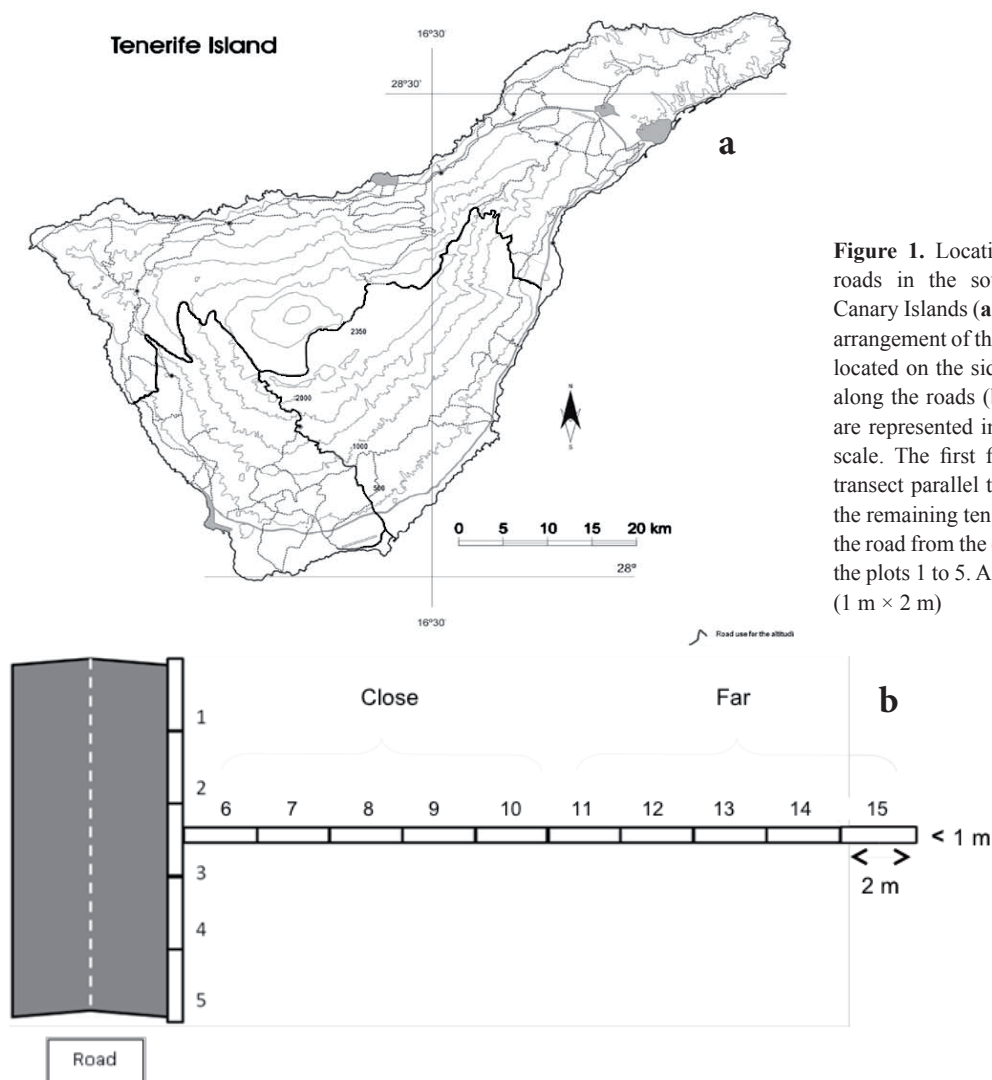


Figure 1. Location of the three sampled roads in the southern part of Tenerife, Canary Islands (**a**) and representation of the arrangement of the 15 plots in the T-transect located on the side of each sampling point along the roads (**b**): the road and the plots are represented in a schematic way, 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 m × 2 m)

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 \times 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 (α_{Plot} , α_{Section} , α_{Transect} , α_{Road}), that summed to the differentiation diversities for the corresponding spatial scales (β_{Plot} , β_{Section} , β_{Transect} , β_{Road}) 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, refer to Figure 1 in Chiarucci et al. 2008). In a hierarchical sampling design with $i = 1, 2, 3, \dots, m$ 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:

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

while for each lower sampling level as

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

Then, the additive partition of diversity is

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

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 out of 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 the Electronic Appendix. 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%), *Pteroccephalus lasiospermus* (11.8%) and *Wahlebergia 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

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 χ^2 distribution; *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

	Model Fitting	Coefficient values and signs	D^2_{adj}	Likelihood ratio test Linear vs. Polynomial Fit (χ^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	

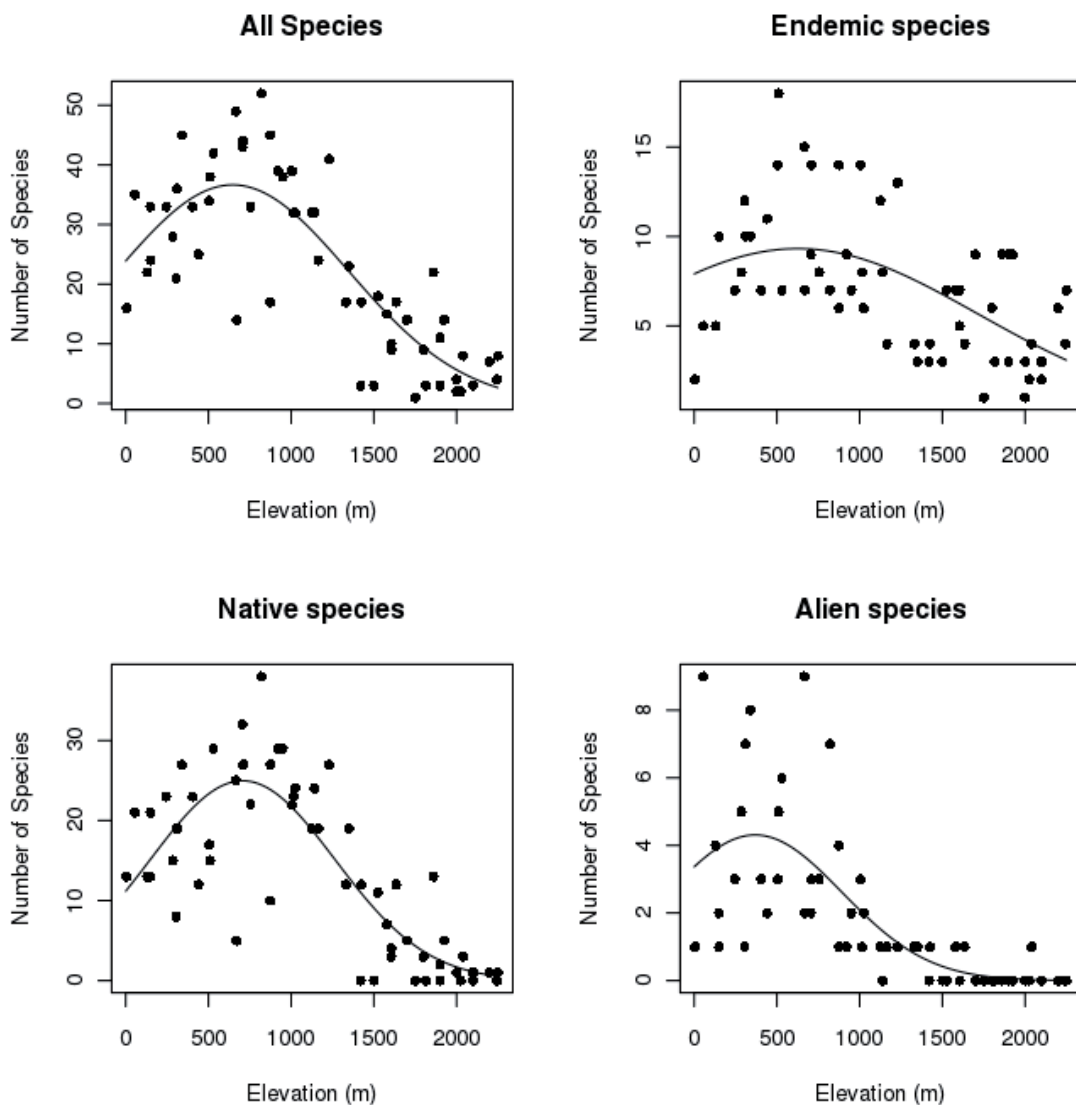


Figure 2. Species richness patterns at the whole transect scale, in relation to the elevation for the four groups of plants considered in the analyses. Continuous lines represent the best descriptive model relating elevation to each species group.

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.

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						

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.

At the transect scale, 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, al-

though 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 × Section, Figure 3) was significant for native

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.

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

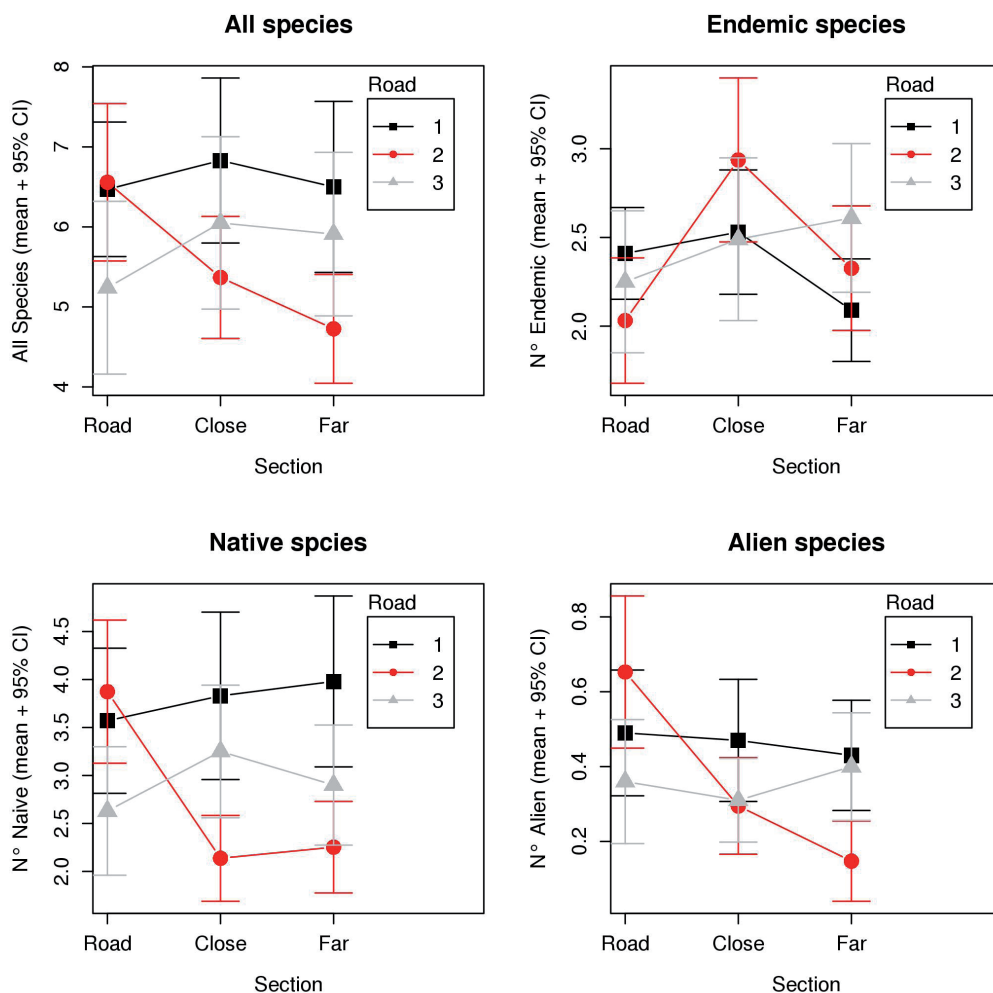


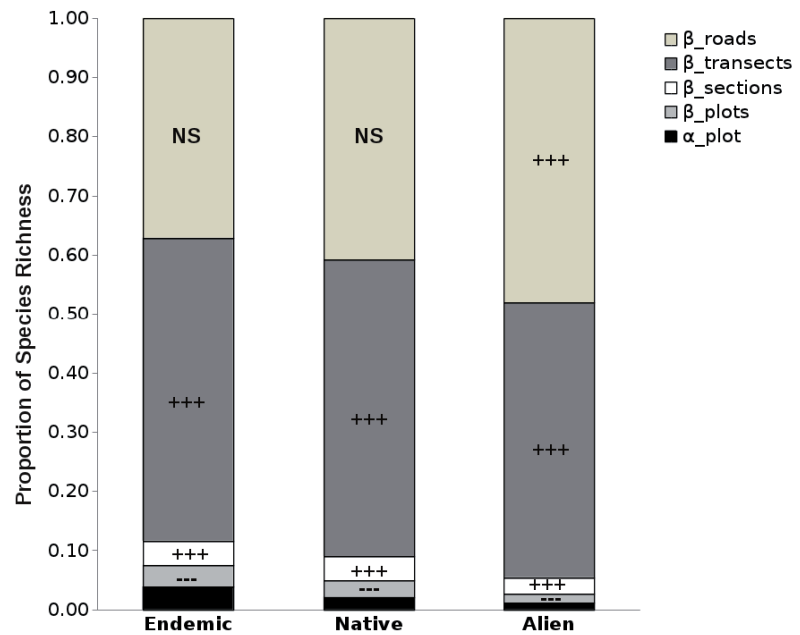
Figure 3. Analysis of the Road × Sector interaction for the four groups of plants analysed using univariate permutational analysis of variance. Significant interactions occurred for endemic, native, and alien species (see Table 2).

and alien species: the testing of Road × Section interaction showed that, on average, the distribution of the total number of plant species (all 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, 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 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 represent-

Figure 4. Percentage of total plant species richness explained for 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).



ing 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 anthropogenic 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. 2014). Assessing patterns of plant species richness along roads and elevation gradients can provide important insights into the effects of anthropogenic activities on plant communities, especially as far as island and mountain ecosystems are concerned. A 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., Fernández-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. 2014). 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), 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, species might have been introduced 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. 2014). Beside 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 previ-

ous 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 Frissell 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 β_{Transect} and β_{Road}), 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 ($\beta_{\text{Transects}}$), 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, β_{Roads} 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 β_{Roads} 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 constraints (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 facilitated by the disturbance regime associated with roads and distinguish between species that can cope with broad environmental conditions (naturalized and invasive species) from those that, despite being introduced and spread even at consider-

able 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 hypotheses on the causes of the spread of invasive species in resident communities along distance gradients perpendicular to roads should be tested.

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Electronic Appendix

List of plant species recorded along the altitudinal gradient.
The file may be downloaded from www.akademai.com.