

How do alien plants distribute along roads on oceanic islands? A case study in Tenerife, Canary Islands

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Abstract Islands are paradigms of the pervasive spread of alien plants, but little work has been done assessing pattern and cause of the distribution of such plants in relation to roads on oceanic islands. We studied richness, composition, and distribution of alien plants and compared them with native species along roads on Tenerife (Canary Islands). We studied a single road transect that sampled two contrasting wind-facing aspects (leeward versus windward) and ran from coastal *Euphorbia* scrubland through thermophilous scrubland to Makaronesian laurel forest at the top of a mountainous massif. We evaluated the effects of

elevation, aspect, distance to urban nuclei, and several road-edge features (including road-edge width and management—implying disturbance intensity), using regression models, analysis of variance, and multivariate ordination methods. Richness of both endemics and native nonendemics was explained by elevation (related to well-defined vegetation belts), steepness of the edge slope, and cover of rocky ground. Despite a short elevational gradient (0–650 m), we found clear altitudinal zonation by biogeographic origin of both nonendemic natives and aliens, and altitudinal distribution of aliens followed the same zonation as that of natives. Alien species' richness was related to management intensity determining edge disturbance, road-edge width, and distance to the nearest urban nuclei (propagule sources). Different variables explained distribution patterns of natives, endemics, and aliens along roadsides on leeward and windward aspects. Altitude and aspect also had a strong influence on the frequency of life strategies (woody species, annuals and biennial/perennial herbs) of roadside plant communities. Due to harsher environmental filters operating on the leeward aspect, alien species were distributed along the altitudinal gradient in apparent consistency with general biogeographical affinities. Tropical/subtropical taxa showed exponential decrease with increasing elevation, Mediterranean taxa showed a unimodal response (i.e., maximum richness at mid elevation, minimum at the extremes of the gradient), and temperate taxa showed linear increase with elevation. Native but nonendemic species followed

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analogous trends to those of aliens. This suggests climatic matching as a prerequisite for successful invasion of this topographically complex island. Other road traits, such as edge width, slope steepness, soil cover, and road-edge disturbance intensity may play a complementary role, at a more local scale, to shape the distribution of alien plants on these island roads.

Keywords Roadside vegetation · Species richness · Aspect · Ordination · Climate matching · Tenerife

Introduction

Invasive plants are undoubtedly among the leading causes of species decline, biodiversity loss, and landscape transformation worldwide (D'Antonio and Vitousek 1992; Vitousek et al. 1997; Mack and D'Antonio 1998). In many instances, oceanic islands have proven to be more fragile than continental areas to alien plant invasions (Wilson et al. 1992; Simberloff 1995; Lonsdale 1999). The mode of dispersal and the distance to source areas are main determinants of distribution of aliens on oceanic islands (Ridley 1930; Davis et al. 2000). Processes at the ecosystem scale (competition and anthropogenic or natural disturbance) may cause or favor the spread of aliens and, hence, reduce native and overall species diversity on islands (Dukes and Mooney 1999; Levine et al. 2003; Whittaker and Fernández-Palacios 2007). Thus, transportation infrastructure is becoming increasingly important at all scales, permitting aliens to reach otherwise remote and undisturbed areas, and heavily changing environments along and across the road corridors (Forman and Alexander 1998; Spelleberg 1998; Trombulak and Frissell 2000). Roads are a major source for aliens to invade natural areas, especially for generalist species with short life cycles and high reproductive ratios (Parendes and Jones 2000; Pauchard and Alaback 2004; Dietz and Edwards 2006).

It has been frequently found that road-edge vegetation shelter a great number of both native and alien species and that species richness along edges is often higher compared with adjoining areas (Ullmann and Heindl 1989; Ullmann et al. 1995). Edge type has been shown to explain significant variation in alien-species

richness of roadside communities (With 2002; Pauchard and Alaback 2006). However, roadsides also act as refuges for rare and endangered species (Quintana-Ascencio et al. 2007). In oceanic islands, few works have evaluated the factors responsible for distribution of alien plants in relation to roads (Wester and Juvik 1983; Hulme 2004; Arévalo et al. 2005).

On the Canary archipelago, the road network has grown dramatically in the last four decades (and continues expanding), situating the islands amongst the most heavily roaded European territories (ca. 6 km/km² including unpaved roads; Fernández-Palacios and Martín Esquivel 2001). Apart from road-edge and other road effects, elevation, area, and topography are constantly invoked as factors driving the structure and distribution patterns of plants on islands (Rejmánek et al. 2005). Elevation, in relation to stratification of climatically contrasting ecosystems, and distance to urban nuclei, as propagule sources, have been identified as important factors explaining distribution of alien and native species along roads on the Canaries (Arévalo et al. 2005). Topography has been found to determine species richness and composition from global (Kreft and Jetz 2007) to local scales (Badano et al. 2005) but has not been related to variation in roadside communities on islands. Preadaptation and inherent resistance of the recipient community (through competence and environmental filters) (Wilson et al. 1992; Daehler 2005) interact with the above island features to shape the alien community composition and distribution. Furthermore, the road-divided ecosystem may present different climatic regimes varying in suitability for alien establishment, depending on the alien's region of origin, which can affect alien invasion success (Jiménez et al. 2008).

We studied alien and native-species richness, composition, and distribution along a road transect that runs from coast to summit in a mountainous area on eastern Tenerife (Canary Islands). The road traverses stands of the three major ecosystems in that part of the island (coastal scrub, thermophilous scrub, and laurel forest) and runs through contrasting topographical aspects (a humid northern or windward aspect and a dry southern or leeward aspect). Elevation, and hence ecosystem stratification, and aspect strongly shape native plant communities; so we studied whether such effects occur on the alien plant community as well. Specifically, we assessed

the effects of (a) elevation, (b) aspect, (c) road-edge characteristics (affecting substrate condition due to road maintenance), and (d) distance to urban nuclei (alien propagule sources). In addition, we evaluated the importance of the geographical origin and life forms in the distribution along the altitudinal gradient, for aliens and also for native nonendemic taxa, as the establishment of aliens along roadways may depend to a great extent on the particular climate of the traversed ecosystem and its resemblance to the climate of the alien's region of origin (i.e., climate matching, see e.g. Jiménez et al. 2008).

Material and methods

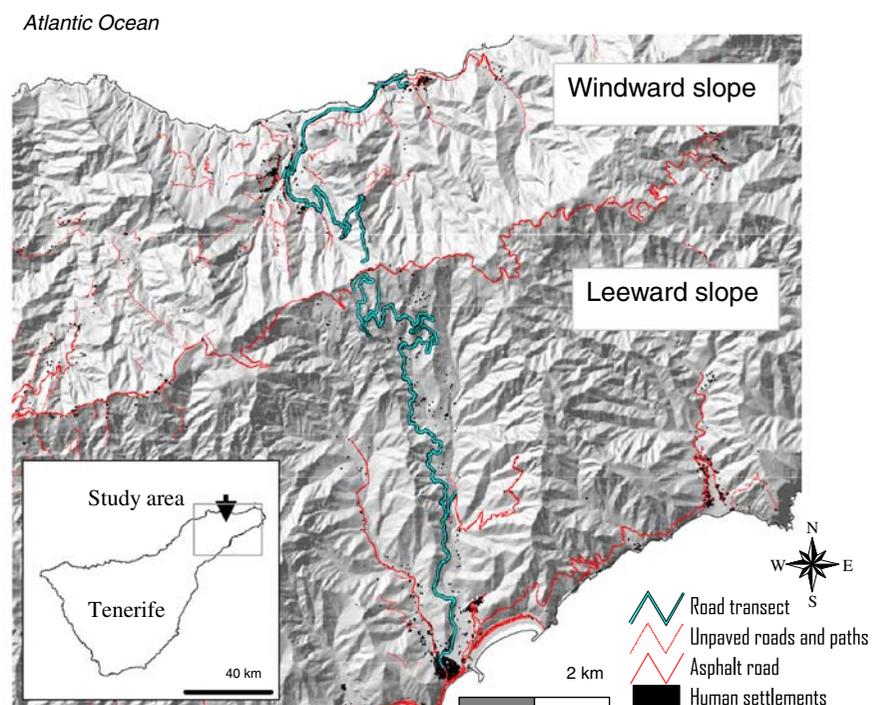
Study area

Field work was conducted in the Anaga massif in northeast Tenerife (Canary Islands) (Fig. 1). We studied a road transect that ran from the coast level on the leeward aspect (San Andrés village), climbed up to the massif ridge (at ca. 4 km in straight line from the leeward coast), and then proceeded through the windward aspect down to the north coast (at ca.

2 km from the massif ridge to the windward coast) in Taganana village. Selection of this single transect, instead of studying two or more comparable roaded areas that should render wider generalizations and sounder conclusions, was dictated by several reasons: (a) We did not know any other road in Tenerife simultaneously traversing, in its natural altitudinal sequence, the three vegetation belts studied here (coastal *Euphorbia* scrubland, thermophilous scrubland, and Macaronesian laurel forest). (b) There is a previous study (Arévalo et al. 2005) evaluating two road transects from coast to summit in two different islands. These road segments, however, could not traverse all the representative vegetation belts because of generalized disturbance of the territory at mid elevations. Moreover, in that study, no variation in aspect was assessed. (c) The road climbs neatly through three native vegetation belts over a short distance and affects two contrasting aspects.

The total length of the road transect was 21.3 km, with 11.8 km on the leeward aspect and 9.5 km on the windward aspect. The leeward and windward parts of the transect encompassed elevation gradients from 0 to 650 m and from 0 to 550 m a.s.l., respectively. On the leeward side, the only village

Fig. 1 Study area and road transect in east Tenerife



is at the coastal line and, consequently, distance to human settlements increase with altitude. On the windward side, the main urban area is Taganana, which is located 3.4 km from the coast (center of the village). A small settlement also appears at the lower end of the transect (Roque de Las Bodegas). The asphalt road on both aspects is 7 m wide on average.

The climate is semiarid to humid Mediterranean type, with mean annual temperature reaching 19°C at the windward coast, 21°C at the leeward coast and about 14°C at the summit. Annual and daily fluctuations of temperature are small due to the subtropical climate. Mesoclimate is affected by the trade winds that create a contrast between the northern or windward aspect (more humid and cloudy) and the southern or leeward aspect (more arid and cloudless). Mean annual precipitation reaches 900 mm in the laurel forest at about 800 m a.s.l. (doubled by fog drip) and 250–300 mm in the coastal zone (Kämmer 1974).

Strong variation in altitude and aspect, which define local mesoclimatic zones and land use, are primary factors in structuring both native and alien plant communities on the Canary Islands (Whittaker and Fernández-Palacios 2007). On Tenerife, the vegetation is structured into five main altitudinal belts: succulent coastal scrub, thermophilous woodland, laurel forest or *laurisilva*, Canarian pine forest, and summit or high-mountain scrub. The road progressed through the first three ecosystems, reaching an altitude of 1,024 m. The succulent scrub is formed by succulent bushes about 0.5–2 m tall, with *Euphorbia* species (*E. canariensis*, *E. balsamifera*, and *E. lamarckii*, the latter in the lowest and more arid patches) accompanied by other shrub species (*Aeonium* spp., *Kleinia neriifolia*, *Lavandula* spp., etc.), grasses, and geophytes. The thermophilous woodland is a taller (up to 3 m) and denser diverse community of shrubs such as *Artemisia thuscula*, *Globularia salicina*, *Jasminum odoratissimum*, *Olea cerasiformis*, and *Periploca laevigata* interspersed with *Euphorbia* and grasses. The laurel forest is dense and diverse, with a canopy (up to 10–15 m tall, 80–100% cover), formed by *Laurus novocanariensis*, *Myrica faya*, *Erica arborea*, and *Ilex canariensis*, plus other less abundant trees, some ferns (*Asplenium onopteris*), bushes (e.g., *Plantago arborescens*), and annuals. The coastal scrub occupies larger areas on the leeward aspect, whereas the laurel forest is better

represented on the windward aspect (Arco-del et al. 2006). The thermophilous scrub is generally the most degraded ecosystem on both aspects.

Data collection and vegetation sampling

We studied vegetation and habitat structure along roadsides along the altitudinal gradient between March and June 2006. We made surveys establishing one plot on each side of the road every 50-m elevation. Plots were rectangles of 50 m² (10 m parallel and 5 m perpendicular to the road edge, following the methods of Arévalo et al. (2005) and Delgado et al. (2007). In total, we sampled 22 and 28 plots at the windward and leeward aspects, respectively. On each plot, we recorded all vascular plant species (annuals included) and visually assigned semiquantitative cover-abundance classes in the following manner: 1, traces; 2, <1% cover; 3, 1–2%; 4, 2–5%; 5, 5–10%; 6, 10–25%; 7, 25–50%; 8, 50–75%; 9, >75%; 10, 100%. We also noted plot universal transverse mercator (UTM) coordinates, elevation (m), exposition (1–360°), slope (°) (with a clinometer), degree of roadside management (signs of recent cutting of vegetation and planting of trees and woody species: low, medium, high), influence of trampling (low, medium, high) and trash (presence of organic/inorganic rubbish in the plot: low, medium, high), horizontal edge width (m), and distance to nearest large urban nuclei (km, as measured on the road as distance traveled by car; we did not consider the few smaller agricultural houses scattered along the road). Furthermore, we recorded cover of rock (geological basement), stones, bare soil, canopy, litter (necromass, fallen leaves), and total vegetation cover as percentage classes (Table 1).

Plant-species identification and classification

We classified taxa according to their chorological status, biogeographical origin, and life form. We distinguished the following four chorological groups: (1) Canary Island endemics, (2) nonendemic natives, (3) certainly introduced, and (4) probably introduced, regardless of their invasive behavior. This classification was based on recent checklists for the whole archipelago (Acebes et al. 2004) and for El Hierro Island (von Gaisberg 2005; Stierstorfer 2005).

Table 1 Mean values of habitat variables and results of the nonparametric Kolmogorov–Smirnov test to evaluate the effect of aspect (leeward/windward) on roadside variables

Variable	Leeward		Windward		Z	P value
	Mean	Standard error	Mean	Standard error		
Exposition (°)	128.0	10.5	215.5	29.8	2.108	< 0.001
Slope (°)	20.5	3.0	23.9	4.8	0.615	0.843
Vegetation cover (%)	72.5	4.1	67.3	4.9	0.558	0.914
Litter cover (%)	8.7	2.2	3.7	0.7	0.900	0.392
Soil cover (%)	30.0	6.0	33.0	5.8	0.729	0.662
Rock cover (%)	18.4	6.0	31.8	7.2	1.368	0.047
Stone cover (%)	13.5	2.3	12.0	2.2	0.672	0.757
Canopy cover (%)	14.8	4.7	1.8	1.1	0.877	0.425
Trash (low,medium, high)	2.1	0.1	2.2	0.1	0.593	0.874
Trampling (low, medium, high)	1.8	0.1	2.3	0.1	1.219	0.102
Road-edge width (m)	1.14	0.21	0.32	0.14	2.621	< 0.001
Road-edge management (low, medium, high)	1.9	0.2	2.3	0.1	1.379	0.045
Distance to urban nuclei (km)	5.243	0.709	2.223	0.238	2.006	0.001

Z estimator of the statistical test, significant differences in bold

All introduced naturalized aliens, as well as native nonendemics, were classified according to their biogeographical origin following Hohenester and Welss (1993); Schönfelder and Schönfelder (1997, 2002); Acebes et al. (2004), and Stierstorfer and von Gaisberg (2005). We distinguished three different groups of origin: (1) subtropical and tropical species, (2) Mediterranean species; and (3) temperate species. A list of all plant species sampled is available from M.A.A.

Statistical analysis

To check for spatial autocorrelation between the two plots on opposite sides of the road, we compared differences of richness for each species group between these two plots and differences between pairs of plots that were separated 50 m in altitude. As we could not detect significant differences between means of the two groups (tested by nonparametric Mann–Whitney *U* test), we considered all plots as independent samples (total richness: $U = 175$, $P = 0.57$; endemic species: $U = 174$, $P = 0.57$; native species: $U = 173$, $P = 0.52$; introduced species: $U = 127$, $P = 0.07$).

We applied nonparametric Kolmogorov–Smirnov test to check for significant differences in roadside variables between leeward and windward aspects. We used linear regression analysis to explore relationships with altitude, distance to urban nuclei, and other

relevant habitat variables. To assess the relationships between species richness of different plant groups by biogeographical origin and aspect (leeward versus windward), we performed regression analyses including quadratic and logarithmic models. We fitted the best functions to the observed distribution of species richness for each origin group with altitude. In each case, we selected models by the highest adjusted coefficient of determination (R^2) and performed an analysis of variance (ANOVA), which returns the value of the *F* statistic and the significance of the test (*P*). For linear function fits, we previously tested for normality and homocedasticity of the dependent variable (species richness). The residuals of each regression were tested for randomness and normality to assess the robustness of the model. Differences of life-form groups between elevation classes were tested using Kruskal–Wallis test, and differences between leeward and windward aspects were tested applying Mann–Whitney *U* test for two independent groups.

We used ordination techniques to explain the variation in species composition [detrended correspondence analysis (DCA)] and to evaluate the multivariate relationships among plant composition and abundance and habitat descriptors along the road transect [canonical correspondence analysis (CCA)] (Gauch 1982). A forward selection procedure by means of Monte Carlo permutation tests (500 iterations for $P < 0.05$) was

carried out to test the significance of variables in CCA. Variables with an ordinal scale were included as dummy variables. We selected scaling on intersample distances and down-weighted rare species by square-root transformation. CCA was performed only with exotic species and on both aspects independently. We followed the statistical procedures of Zar (1984) using the SPSS statistical package (Anon 1990) and the CANOCO package (ter Braak and Šmilauer 1998). Where data were not normal and homocedastic and could not be transformed, we applied nonparametric statistics.

Results

General characteristics: status, life forms, and habitat variables

We recorded 264 plant species. In the 50 plots, we found 63 endemic species (24% of the total number of species sampled), of which 71% were woody (phanerophytes or chamaephytes) and only 9.7% annuals (Fig. 2). Native nonendemic species were the most important in the overall species pool (104 recorded species, or 39%), being dominated by therophytes (60%), phanerophytes (16.3%), and hemicryptophytes (15.4%). Finally, 97 introduced species were recorded (37%). Both certainly and probably introduced species showed a high proportion of annuals (69% and 92%, respectively) but differed considerably with respect to woody species (20% and 4%, respectively). The most common alien species with more than 15% frequency (both aspects) were in this order: *Polycarpon tetraphyllum*, *Rubus ulmifolius**, *Sonchus oleraceus*, *Foeniculum vulgare**, *Medicago polymorpha*, *Bidens pilosa*, *Urospermum picroides*, *Opuntia maxima**, *Conyza bonariensis*, *Erodium malacoides*, *Leontodon taraxacoides*, *Echium*

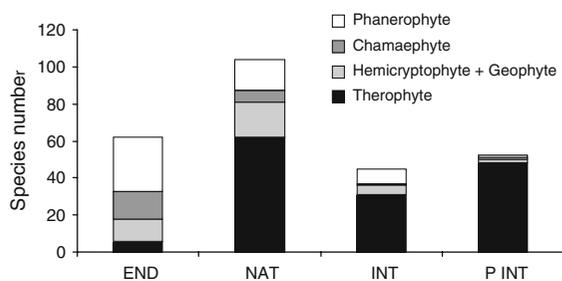


Fig. 2 Life-form distribution within species groups of the overall species pool (abbreviations of species groups in Table 3)

plantagineum, *Ageratina adenophora**, *Agave americana** and *Oxalis pes-caprae**. Species marked with an asterisk are considered invasive (see Appendix).

Life-form distribution changed significantly with elevation (Fig. 3). Considering both aspects and all species, therophytes were more abundant in the coastal areas, whereas percentages of hemicryptophytes and phanerophytes were highest above 400 m a.s.l. Chamaephytes and geophytes showed no trend. Therophytes were more important leeward than windward, and chamaephytes were more abundant windward (Fig. 3).

We found significant differences between aspects in exposition, rock cover, road-edge width, edge-management intensity, and distance to urban nuclei (Table 1). On the leeward aspect, roadside habitats were mostly facing east or southeast, whereas they faced northwest or northeast on the windward aspect. Windward roadsides were characterized by higher rock cover, narrower road edges, more intensive roadside management, and shorter distance to settlements. A generally steeper slope in the windward road may be a cause for a narrower road edge and hence also for a smaller richness of aliens (Table 1).

Species richness

Overall richness was higher on the leeward (226 species) than on the windward (157 species) aspect. Thirty-eight species were found exclusively windward and 107 leeward, whereas 119 were common on both

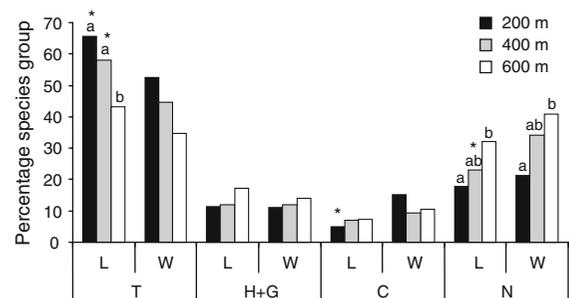


Fig. 3 Life-form distribution of all species according to elevation (classes: 200 = 1–199 m; 400 = 200–399 m; 600 = 400–650 m) and aspect (L leeward; W windward). Differences between elevation classes were tested using Kruskal–Wallis test (different letters indicate significant differences between groups at $P < 0.05\%$). Differences between leeward and windward aspect for each altitudinal belt were tested applying the Mann–Whitney U test (* $P < 0.05\%$, ** $P < 0.01\%$). (T therophyte, H + G hemicryptophyte and geophyte, C chamaephyte, N nanophanerophyte)

aspects. We found significantly higher species richness of native taxa ($t = 4.471$, $P < 0.001$), introduced taxa ($t = 2.110$, $P = 0.040$), and overall richness ($t = 3.760$, $P < 0.001$) on leeward than on windward roadsides (Fig. 4). Native nonendemic species were most abundant in roadside plots, followed by introduced species. Endemic species were relatively scarce along edges (an average of 8.4 species on leeward and 7.5 species on windward slopes) and showed no significant difference between slopes.

On the leeward aspect, rock cover was the best explanatory factor for local overall species richness, whereas endemic-species richness was positively related with rock cover and slope degree (Table 2). Native nonendemic richness was negatively correlated with altitude, distance to settlements, and management intensity. Road-edge width was the best predictor for the total richness of all introduced species. The distribution of introduced species was best explained by road-edge width and soil cover. Probably, introduced species showed no relation with the studied variables.

On the windward aspect, overall species richness was best explained by management intensity and endemic richness by altitude and rock cover (Table 2). Richness of native nonendemic species was not correlated with any roadside variable. Richness of all three groups of introduced species (certainly introduced and probably introduced) was significantly related to local management intensity and distance to urban nuclei.

Relationships of plant origin groups with altitude

From the total pool of introduced species, 51% was of tropical or subtropical, 36% of Mediterranean, and 11% of temperate origin. In contrast, 73% of probably introduced species was of Mediterranean, 10% of temperate, and only 6% of tropical/subtropical origin;

71% of native species was of Mediterranean, 16% of tropical/subtropical (mostly Saharo-Sindic), and 8% of temperate origin.

Altitudinal distribution along the road edge of nonendemic native species with a Mediterranean origin fitted a quadratic curve, with maximum richness at mid elevations (300 m a.s.l.) on both aspects (Fig. 5; Table 3). On the leeward aspects, introduced species with Mediterranean origin followed similar distribution, whereas probably introduced species showed no trend for this biogeographical group. Tropical/subtropical species were always more abundant along the coastal roadside and decreased with altitude, fitting a log model on both aspects for native species and for introduced species on the leeward aspect. Temperate (native and probably introduced species) increased toward the mountain ridge, following a linear model on the leeward aspect, but fitted a quadratic distribution on the windward aspect for native species. Regarding the introduced species windward, none of the biogeographical groups fitted significantly to a regression model. Regarding species origin, overall richness followed the same pattern as native species.

Species composition along the elevation gradient

The DCA of all samples and all species (endemic, native, and introduced) revealed the floristic differences between aspects (leeward versus windward) on the second axis, which separates samples especially in the lower part of the road transect, and the strong floristic gradient on the first ordination axis, which correspond to the elevation or climatic gradient (Fig. 6). Ordination showed that the leeward gradient was stronger (longer distance between samples spread more to the left side) than the windward one, where samples were more clumped in the center of the ordination. Species present in the lower part of the leeward gradient but absent windward (including

Fig. 4 Variation in plant-species richness per plot between aspects (mean + 1 standard deviation)

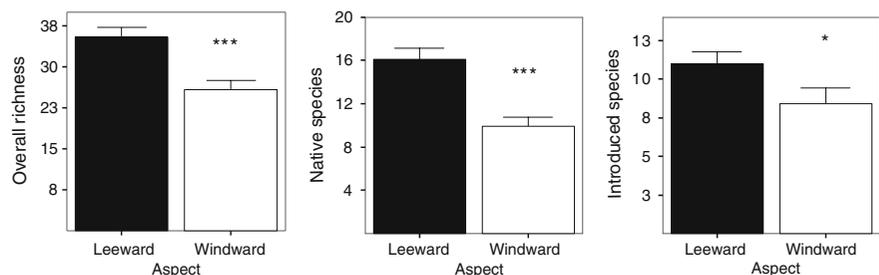


Table 2 Results of the linear regression analysis with plant-species richness as dependent variables and each environmental factor as independent variables for leeward and windward slope (only independent variables showing significant results are shown)

Variable	Leeward slope				Windward slope							
	Total	End	Nat	Tot int	Int	P int	Total	End	Nat	Tot int	Int	P int
Elevation	-0.331	0.015	-0.457*	-0.194	-0.301	-0.067	0.069	0.459*	-0.226	0.069	0.001	-0.109
Slope	0.302	0.441*	0.282	-0.021	-0.086	0.029	-0.074	0.165	0.001	-0.261	-0.169	-0.279
Rock cover	0.409*	0.591***	0.292	0.102	-0.093	0.202	0.054	0.468*	-0.152	-0.165	0.009	-0.265
Soil cover	0.056	-0.030	-0.079	0.270	0.381*	0.118	0.233	-0.288	0.339	0.342	0.161	0.425*
Road-edge width	0.247	-0.264	0.301	0.411*	0.463*	0.259	0.032	0.079	-0.188	0.148	0.068	0.180
Distance to urban center	-0.358	0.011	-0.492**	-0.207	-0.316	-0.074	-0.173	0.203	-0.066	-0.043	-0.503*	-0.246
Road-edge management	-0.205	-0.094	-0.403*	0.180	0.084	0.124	0.578**	0.365	0.191	0.512*	0.455*	0.453*

Corresponding correlation coefficients are shown

Total total richness species, *End* endemic species, *Nat* native nonendemic species, *Tot int* total introduced species, *Int* introduced species, *P int* probably introduced species
* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

native or endemic shrub species common to the succulent scrub): *E. canariensis*, *E. balsamifera*, *E. lamarckii*, *Plocama pendula*; small native shrubs: *Fagonia cretica*; native annuals: *Misopates orontium*, *P. afra*, *Spergularia fallax*, *Stipa capensis*; introduced annuals: *Datura innoxia*, *Emex spinosa*, *Linum strictum*, and *Portulaca oleraceus*.

On the leeward side, the CCA for all introduced species clearly separated three groups of plots corresponding to the vegetation belts, with increasing altitude and distance to nearest villages along the axis I (Fig. 7). The first axis represents a strong gradient in elevation (Monte Carlo permutation test, $F = 2.13$, $P = 0.002$) and distance to urban areas ($F = 3.77$, $P = 0.002$). The other two significant factors affecting introduced species composition were aspect ($F = 1.37$, $P = 0.040$) and soil cover ($F = 1.33$, $P = 0.044$). All other variables were not significant.

On the windward aspect, we found a weaker gradient of exotic species, with a 15.3% variance accounted for by the first axis (eigenvalue = 0.536) and 14.2% by the second axis (eigenvalue = 0.497) of the CCA (Fig. 7). Elevation ($F = 1.93$, $P = 0.002$), distance to urban nuclei ($F = 1.55$, $P = 0.01$) and edge management ($F = 1.57$, $P = 0.014$) were the only significant variables. Besides the three coastal sites (1D, 1C, and 2D), which represented a very different halophytic vegetation and were clearly separated by the CCA ordination, composition of exotic species was more homogeneous on the windward than on the leeward aspect.

Discussion

Environmental factors

Results showed that whereas endemic and native nonendemic species, physiographic factors, and the underlying climatic aspects best explained richness, exotic richness was related to disturbance factors windward and to road-edge characteristics leeward. However, we detected considerable differences between aspects regarding the significant explanatory variable that was correlated with each species group.

We found a positive relationship between richness of endemic species and rock cover, partly due to association with steep slopes. Highly inclined roadsides showed usually low soil cover and a high percentage of surface rocks, which is suitable habitat for native rupicolous

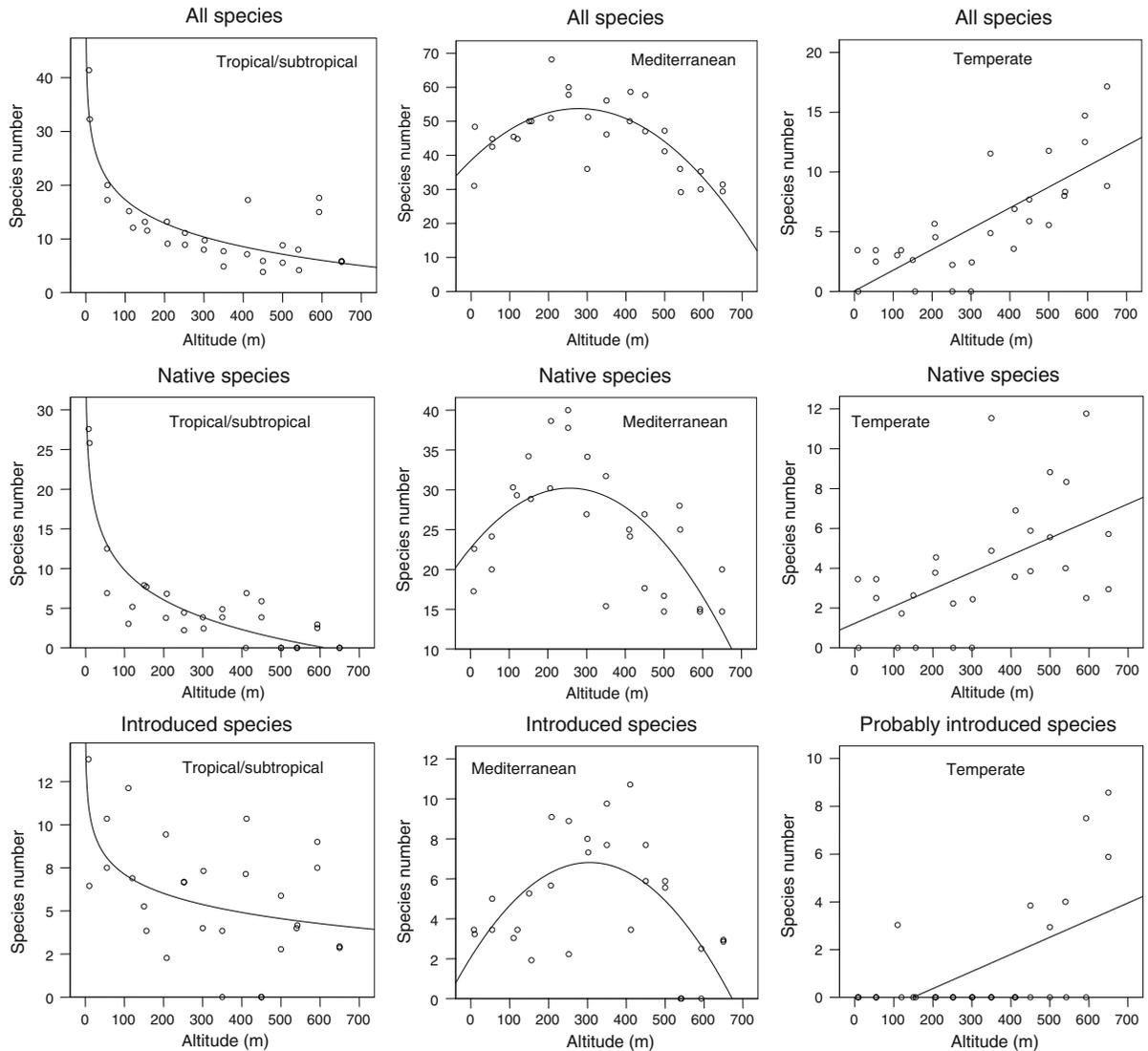


Fig. 5 Regression curves for relative species richness (percentage of total richness per plot) by biogeographical origin along the road-elevation gradient on the leeward slope

(nonsignificant regressions and groups with low species number are not shown; see regression results in Table 3)

communities or, in the case of a disturbed site, a favorable habitat for recolonization by these endemics. In a similar study on Tenerife with a much longer altitudinal road transect (sea level up to 2,300 m a.s.l.) but generally with lower roadside inclination, endemic-species richness was not correlated to rock cover but was negatively correlated to soil cover (Arévalo et al. unpublished data).

It has been frequently demonstrated that composition and richness of plant species respond to altitudinal gradients (Ullmann et al. 1995; Pauchard and Alaback

2004; Becker et al. 2005). Altitudinal distribution of both native and alien plant species is largely related to environmental stress gradients dependent on altitude (Alpert et al. 2000; Godfree et al. 2004). Mesic environmental conditions such as high humidity, low thermic and hydric stress, and high productivity are largely responsible for quick establishment and dispersal of aliens on islands (Whittaker and Heegaard 2003). On Tenerife, these favorable conditions for exotic plant invasion were found at about 800–1,000 m

Table 3 Regression results (curve fitting) of altitude with plant-species number with respect to biogeographical origin, status, and island aspect

Species origin (model)	Overall richness			Natives			Introduced			Probably introduced		
	Model	R ²	P	Model	R ²	P	Model	R ²	P	Model	R ²	P
Leeward slope												
Tropical/subtropical species	Log	0.630	<0.001	Log	0.833	<0.001	Log	0.267	0.005	– ²	–	–
Mediterranean species	Quad.	0.585	<0.001	Quad.	0.450	0.001	Quad.	0.381	0.002	Quad.	0.024	0.743
Temperate species	Linear ^a	0.590	<0.001	Linear ^a	0.290	0.003	– ^b	–	–	Linear ^a	0.335	0.001
Windward slope												
Tropical/subtropical species	Log	0.227	0.025	Log	0.769	<0.001	Linear	0.088	0.181	Linear	0.051	0.312
Mediterranean species	Quad.	0.304	0.032	Quad.	0.289	0.039	Quad.	0.175	0.160	Quad.	0.037	0.701
Temperate species	Quad.	0.456	0.003	Quad.	0.384	0.01	Linear	0.057	0.29	Linear	0.001	0.872

^a Dependent variable fulfilled normality (Kolmogorov–Smirnov test, K-S = 0.131, $P = 0.200$) and homocedasticity (Levene statistic = 0.441, $P = 0.510$)

^b Low number of species (<5) in this group

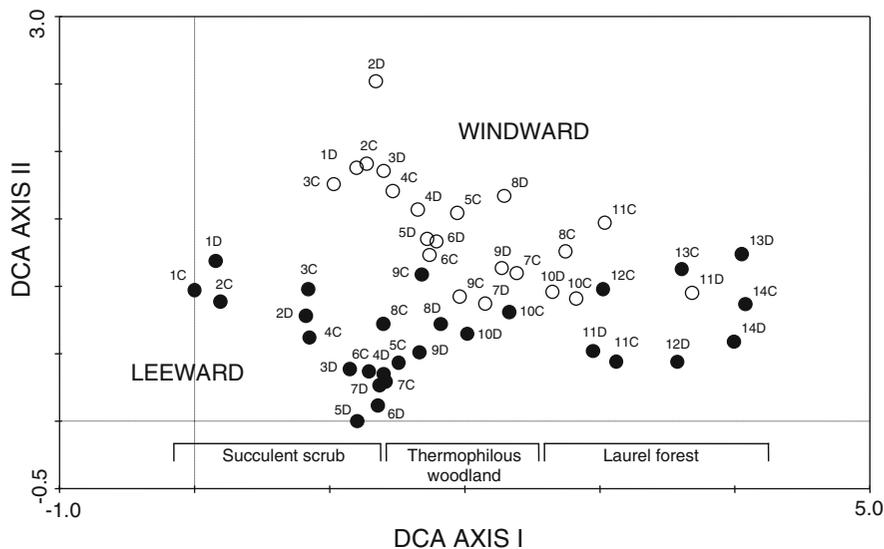


Fig. 6 Ordination by detrended correspondence analysis (DCA) of all roadside plots and all species (endemic, native, and introduced). Potential vegetation types are shown along the elevation gradient. *Filled circles* leeward plots, *open circles* windward plots. *Numbers* represent sites beginning at the coast, *letters* side-of-the road sampled, *C* right side, *D* left side.

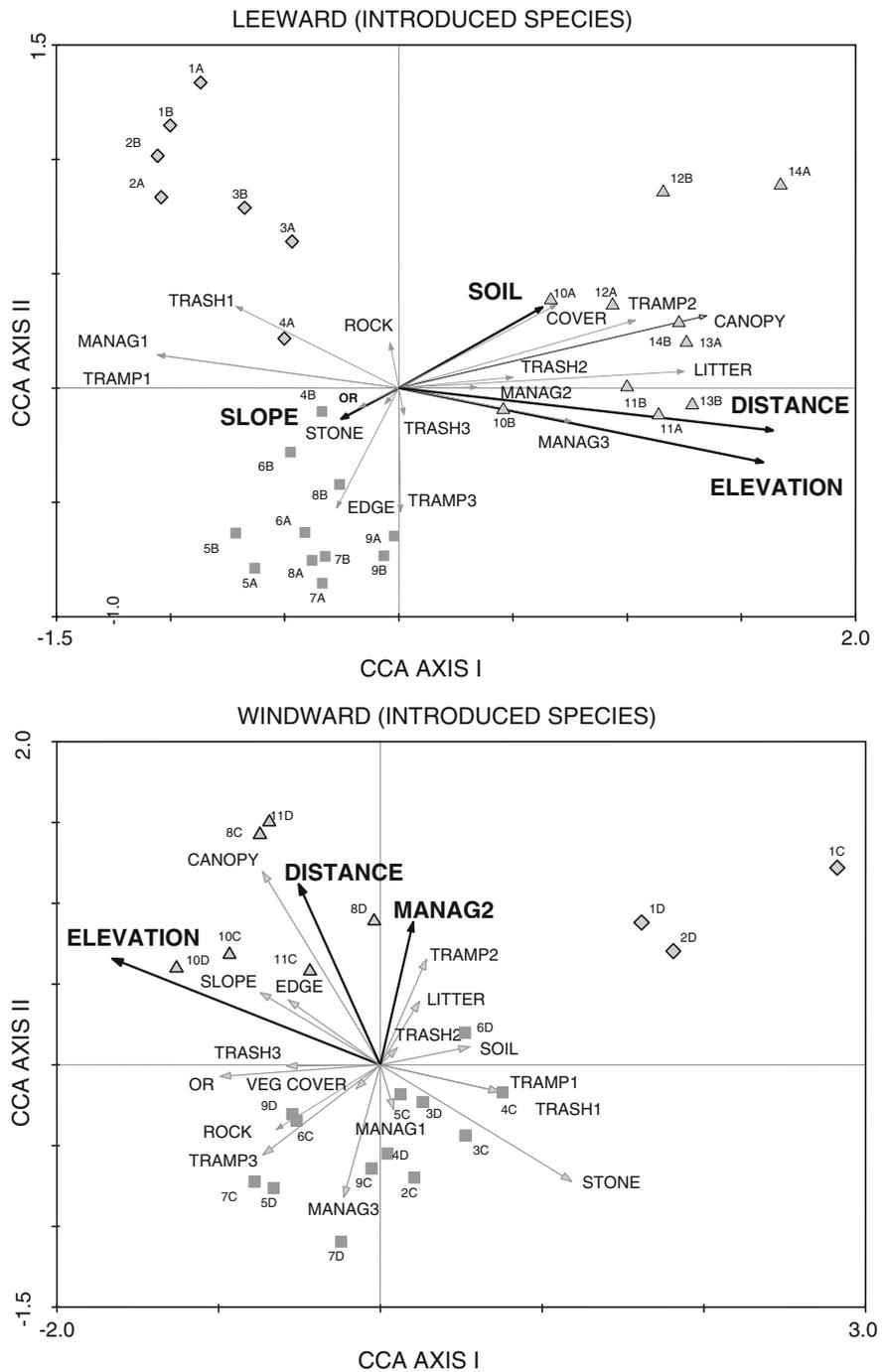
a.s.l. on the leeward aspect, where a maximum number of native and alien-species richness were recorded (Arévalo et al. 2005). Consequently, native- and alien-species richness was positively correlated with altitude in the lower part of that road transect, corresponding to a precipitation gradient from coast to mid altitudes. At high elevations, thermic and hydric stress reduces the

Outlier sample 1C at windward, representing specific halophytic vegetation by few species with high abundance value, was not included in the analysis. The two first axes accounted for 17.3% of the total variance of species data. Eigenvalues were 0.525 and 0.220, respectively. Gradient length was 4.077

number of successful colonizations of exotics, a distribution pattern observed also in other parts of the world (Godfree et al. 2004; Pauchard and Alaback 2004; Becker et al. 2005).

In contrast, in our study altitude was negatively related with native-species richness along road edges on the leeward aspect, and introduced species were not

Fig. 7 Canonical correspondence analysis of ecological variables and road-study plots. For the canonical correspondence analysis (CCA) ordination at the leeward aspect, the first axis accounted for 19.1% of the variance in the species–environment relationship (eigenvalue = 0.689). The second axis accounted for 11.5% of the variance (eigenvalue = 0.416)



correlated with altitude. Therefore, altitude per se did not determine alien-species richness, as other interacting variables such as topography have an influence at the island scale (i.e., aspect determines influence of dominant wind regimes on the plant communities).

Biogeographical origin and life forms of species

The results of this study indicate that the observed distributions of both native, nonendemic, and introduced plants along the altitudinal gradient vary in

correspondence with their biogeographical origin and environmental tolerance, as described in similar investigations on islands (Wilson et al. 1992; Daehler 2005). On Tenerife and Gran Canaria, Mediterranean species clearly show an optimum at mid altitudes (800–1000 m a.s.l.) under a typical Mediterranean climate, whereas non-European species, mostly of subtropical and tropical origin, dominate in the lower regions with a subtropical semiarid climate (Arévalo et al. 2005). Their ecological ranges are probably limited by low temperatures. Temperate species, which are, in general, more tolerant to thermic stress but less tolerant to hydric stress, were most abundant at high elevations (1,200–1,500 m a.s.l.). Daehler (2005) observed similar patterns on Hawaii, where the relative importance of temperate species increased strongly above 1,400 m a.s.l., whereas tropical species decreased. Our findings strongly support the biogeographical approach to plant invasion as it has been stressed recently (Hierro et al. 2005).

Life-form spectra were also strongly influenced by elevation, as therophytes were more abundant in the lower part of the road transect where open shrubland enables the establishment of annuals, not only at the road edge, but also on the adjacent sloping bank covered by native vegetation. Above 400 m a.s.l., structural changes occurred from open shrubland to closed laurel forest. Consequently, phanerophytes increased in importance and annuals were limited to the road edge, probably due to competition for light. Therophytes were more abundant leeward than windward, which can be explained by the wider road edge and the more extended area of succulent *Euphorbia* scrub on that aspect of the massif.

Disturbance and introduced species

The most important factors determining introduced-species richness were disturbance factors such as edge structure, management intensity, and distance to the nearest settlements. Road-edge width seemed to be an important variable explaining richness of overall and introduced species on the leeward aspect. Trampling and mechanical disturbances of the ground usually increase as the edge widens, facilitating the arrival and establishment of exotics, included invasive species such as *Agave*, *Ageratina*, *Nicotiana*, and *Ricinus*. Edge structure can be an important factor for invasion success and the subsequent spread into adjacent native vegetation types (Cadenasso and

Pickett 2001). In relatively homogeneous ecosystems on wide continental areas (i.e., coniferous forests), edge types can be differentiated by type and intensity of disturbance (i.e., undeveloped landscapes versus landscapes affected by natural or anthropogenic fires, mowing, clear-cutting, or wind-throwing) (e.g., Pauchard and Alaback 2006). Contrastingly, our road transect was not affected at a landscape level by any of these types of disturbance. Instead, we found that the alien-plant assemblages on these island road edges were affected at two different scales: (1) by elevation leading to stratified ecosystems (inherent factor), and (2) by the intensity of disturbance (extrinsic factor due to land use and roadside substrate alteration at a local scale).

Distance to nearest urbanization nuclei can be considered a proxy for intensity of propagule pressure, which is one of the most important factors explaining invasion success of alien species (Wace 1977; Wester and Juvik 1983; Williamson 1996; Sakai et al. 2001; Rouget and Richardson 2003; Pauchard et al. 2003; Dark 2004). Although this factor has been confirmed to strongly influence the distribution of exotics on roadsides on the Canary Islands (Arévalo et al. 2005), in our study, only introduced species on the windward aspect responded to this variable. The area around villages is characterized by a more intensive land use and encroachment of different kinds of human impacts, including some grazing by goats and patches of agricultural and abandoned land. All these activities increase the propagule pressure of exotics as well as the abundance of native annuals. On leeward sites, the inverse direction of environmental stress (decreasing with altitude) and distance to settlements (increasing with altitude) could be a reason for no correlation with this disturbance factor.

Management of the edge causing increased disturbance was an important factor determining the introduced species richness on the windward but not the leeward aspect. Road management has been reported to influence road-edge structure by changing substrate and soil type, edge maintenance by cutting of vegetation, and deposition of materials, including propagules from outer areas (Forman et al. 2002).

Roadside soil has been found to favor the invasion of xeric shrub communities by alien plants (Greenberg et al. 1997). In our study, soil cover was the only environmental factor related to the abundance of some

of the three groups of alien species for both aspects, probably due to the high number of annuals in this group. Annuals need superficial fine earth to establish, especially in the semiarid Canarian scrubland, where soils are poorly developed (Otto; unpublished data).

Species composition along the elevation gradient

DCA analysis of all species showed the effect of aspect and elevation on floristic composition of the roadside community. The lower parts of the road transect on both aspects (from coast up to 300 m a.s.l. on the windward and to 400 m a.s.l. on the leeward aspects—thermophilous woodland) presented very different floristic composition. Above 400 m a.s.l., the similarity of local climatic conditions in the upper parts of the transect, and the geographical vicinity, conditioned a higher floristic homogeneity. Results support the idea that the climatic gradient on the leeward side is stronger and extended at the lower end, as species represented in the lowest part of the transect, typical of the succulent scrub, do not appear on the windward side. The regional map of natural potential vegetation (Arco-del et al. 2006), which indicates a wider area for the coastal succulent scrub on the leeward than on the windward side, supports this observation.

CCA analysis of introduced species illustrated that at the leeward or southern aspect, three clearly segregated species assemblages appear according to the location along the first ordination axis (i.e., elevation gradient). These three groups correspond to the altitudinal distribution of main ecosystems, namely, succulent scrub at low elevations, thermophilous woodland at mid altitudes, and laurel forest at the ridge top. The intense compositional gradient for alien assemblages, with a full species turnover, supports the concept that ecological filtering is crucial for invasion success (Godfree et al. 2004; Daehler 2005). On the other hand, distance to urban nuclei, which clearly covaried with elevation, has probably not the same importance on floristic composition in this case.

Intrinsic traits of the altitudinal ecosystems fragmented by roads, such as soil, litter productivity, canopy height, overall plant cover, temperature, and light penetration may determine to some extent the composition of alien species (Delgado et al. 2007). In the upper parts of the transect, the laurel forest interior is a less adequate habitat for sun-loving plants than the open coastal and middle zones, and

alien species able to settle there must have particular adaptations to light restriction and to avoid potential impact of native plant allelochemicals.

Therefore, not only climatic matching, shown by the altitudinal distribution of biogeographical groups of species, but probably also the local combination of other environmental factors (light, soil conditions) and structural parameters (canopy height and cover) of the adjacent vegetation, are responsible for the clear floristic grouping of exotics on the leeward aspect, which was also supported by the observed changes in life form groups with elevation.

Although altitude was the most important variable selected in the CCA on the windward or northern aspect of the island, we found no neatly differentiated exotic plant assemblages with elevation. This exposure is affected by trade winds, which largely override the climatic gradient, the road transect is shorter, and the distance from mountain peak to coastline is smaller. All these factors probably contribute to a more homogeneous floristic composition of aliens. Interestingly, distance by urban nuclei and management intensity not only influence the number of alien species but also the composition of these species on the windward aspect. Both the weaker climatic gradient and the locally stronger influence of human disturbance around the small village within the road transect can explain the lack of climatic matching of exotic species on the windward aspect.

Conclusions

Alien species from diverse geographical origins were highly successful in the colonization of disturbed roadsides within different mesoclimates and recipient vegetation belts. Elevation (surrogate for climate) explained variations in species composition of roadside communities and distribution of biogeographical groups of native nonendemics and aliens. Climatic matching seems to be a prerequisite for establishment and successful invasion of exotic species on oceanic islands, especially where strong environmental filters (such as on the leeward side in this study) prevail (see also Arévalo et al. 2005; Daehler 2005). In addition, on oceanic islands with steep abiotic gradients over relatively short distances and roughed topography, aspect is an important factor. However, elevation was not a good predictor of alien species richness, which

Table 4 Indications for roadside management during road construction and operation

Constructive phase	Operating phase
1. Maintain and preserve original topography, soil, substrate, and adjacent native vegetation to increase ecosystem resistance against invasion	1. Control/eliminate alien foci on roadsides, especially near disturbed places (housing, road filling, road material stocking sites) within natural areas (Forman et al. 2002; Pauchard et al. 2003).
2. Narrow road edge to reduce space for human disturbance/ alien establishment	2. Monitor the semiarid scrubland near the coast, not only high productivity areas of the forest belt; invasion starts from the coast
3. Surface roadsides with autochthonous inert materials (stones/gravel, small fraction of soil substrata) to minimize colonization by herbaceous aliens (Gelbard and Belnap 2003).	

responded to distance to propagule sources in human settlements and local conditions of the road edge. Roadside structure (edge width, slope degree, soil cover) and management intensity also played an important role in the invasion process on a local scale. New and existing island roads would benefit

from applying some good practices suggested by our results (Table 4).

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Appendix

Most frequent introduced plant species

Species	Life form	Origin	Status	Invasive species	Total frequency	Frequency leeward	Frequency windward
<i>Polycarpon tetraphyllum</i>	Th	Tropical/subtropical	P		24	12	12
<i>Rubus ulmifolius</i>	Ph	Mediterranean	P	Yes	23	12	11
<i>Sonchus oleraceus</i>	Th	Mediterranean	P		21	13	8
<i>Foeniculum vulgare</i>	H	Mediterranean	C	Yes	17	6	11
<i>Medicago polymorpha</i>	Th	Mediterranean	P		16	10	6
<i>Bidens pilosa</i>	Th	Tropical/subtropical	C		14	7	7
<i>Opuntia maxima</i>	Ph	Tropical/subtropical	C	Yes	13	11	2
<i>Conyza bonariensis</i>	Th	Tropical/subtropical	C		13	3	10
<i>Leontodon taraxacoides</i>	Th	Mediterranean	C		13	11	2
<i>Urospermum picroides</i>	Th	Mediterranean	P		13	8	5
<i>Erodium malacoides</i>	Th	Mediterranean	C		12	7	5
<i>Echium plantagineum</i>	Th	Mediterranean	P		12	10	2
<i>Ageratina adenophora</i>	H	Tropical/subtropical	C	Yes	11	6	5
<i>Scorpiurus muricatus</i>	Th	Mediterranean	C		9	7	2
<i>Cerastium glomeratum</i>	Th	Mediterranean	P		9	8	1
<i>Picris echioides</i>	Th	Mediterranean	P		9	6	3
<i>Silene gallica</i>	Th	Mediterranean	P		9	5	4
<i>Oxalis pes-caprae</i>	G	Tropical/subtropical	C	Yes	8	2	6
<i>Agave americana</i>	Ph	Tropical/subtropical	C	Yes	8	2	6
<i>Fumaria bastardii</i>	Th	Mediterranean	P		8	4	4
<i>Galactites tomentosa</i>	Th	Mediterranean	P		8	3	5
<i>Stipa neesiana</i>	H	Tropical/subtropical	P		7	7	0
<i>Cotula australis</i>	Th	Tropical/subtropical	C		7	5	2

Appendix continued

Species	Life form	Origin	Status	Invasive species	Total frequency	Frequency leeward	Frequency windward
<i>Bromus madritensis</i>	Th	Mediterranean	P		7	6	1
<i>Galium aparine</i>	Th	Temperate	P		7	3	4
<i>Sonchus asper</i>	Th	Mediterranean	P		7	5	2

Life form: *Th* therophyte, *H* hemicryptophyte, *G* geophyte, *Ph* phanerophyte. Status: *C* certainly introduced, *P* probably introduced. Frequency: number of plots where species present (total number of plots 50)

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