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ORIGINAL PAPER

# Diversity and distribution of the last remnants of endemic juniper woodlands on Tenerife, Canary Islands

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**Abstract** Identifying ecological requirements, species diversity patterns and distribution ranges of habitats of interest is an important task when developing conservation and restoration programs. The Canarian juniper woodland formed by *Juniperus turbinata* ssp. *canariensis* is listed as a priority habitat by the European Union. Although very common in the past, this vegetation type has suffered immense destruction and degradation over the last five centuries on the Canary Islands, especially on the largest most populated island of Tenerife. We evaluated the geographical distribution range of the last remnants of Canarian juniper woodlands on Tenerife and analyzed their ecological status, floristic composition and plant species diversity. Despite the degradation of the original vegetation, we still observed outstanding species diversity. Endemic species richness and number of typical habitat species were best predicted by summer rainfall, which seems to be the limiting factor for this habitat in the lower drier regions. Human disturbance has had a negative effect on endemic species richness but a positive effect on the distribution of alien plants, highlighting the potential threat to this habitat. Ecological characterization and floristic composition were most influenced by climatic factors related to the dichotomy of a humid windward and a drier leeward slope of the island and by altitude. However, vegetation structure and human disturbance also determined species composition. Environmental requirements indicated a circuminsular potential distribution of this habitat. Given the exceptional plant diversity, the scarcity of dense stands and the low protection status, immediate protection of the remaining stands and future restoration programs should be the priority for conservation strategies of this endemic vegetation type.

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## Introduction

The characterization of the ecological status, the analysis of species diversity and the delimitation of the geographical distribution of habitats and plant populations of interest are fundamental in conservation biology (Scott et al. 2001; Linares-Palomino et al. 2010; Bacaro et al. 2011). This also holds true for some juniper woodlands, growing in semiarid regions (Gardner and Fisher 1996; Gauquelin et al. 1999; Muñoz-Reinoso 2004; El-Bana et al. 2010). When restricted to just a few areas, isolated plant populations are more susceptible to climate change, human pressure and to suffering from stochastic events that can threaten their resources and habitats. Consequences might be the loss of biodiversity of associated floras and faunas, including the genetic diversity of the species populations (Thompson 1999). These negative effects are of special concern when target communities are rich in endemic species (El-Bana et al. 2010). Therefore, identifying the geographical range and environmental requirements of rare target species or habitats represents an important tool in conservation planning and biodiversity monitoring.

Endemic plant species richness is known to be high on oceanic islands and is related to multiple factors, such as isolation in time and space from the continent, water-energy-dynamics, environmental gradients resulting in high habitat diversity or environmental heterogeneity, actual size of islands or habitats as well as their historical commonness (Whittaker and Fernández-Palacios 2007; Kreft et al. 2008; Jakobs et al. 2010; Zobel et al. 2011). Furthermore, oceanic islands are particularly prone to invasions by alien species due to their unique ecological and biogeographical conditions (Cronk and Fuller 1995; Denslow et al. 2009). These biological invasions are considered the main threats to native biodiversity (Mack et al. 2000).

On the island of Tenerife (Canary Islands), climatic gradients related to elevation and slope orientation have been identified as the most important factors shaping plant species richness and communities (Fernández-Palacios 1992; Fernández-Palacios and de Nicolás 1995; Whittaker and Fernández-Palacios 2007). In contrast, human activities, such as road infrastructures and land use types, play an important role in the distribution of alien plant species (Arévalo et al. 2005; Arteaga et al. 2009; Arévalo et al. 2010), which has also been reported from other oceanic islands (Jakobs et al. 2010; Kueffer et al. 2010).

Although recent information exists on the estimated potential area of the thermophilous forest, including Canarian juniper woodlands, for each Canary Island based on bioclimatic and phytocoenotic data (Del Arco et al. 2006a) and the diversity of its species pool (Domínguez-Lozano et al. 2010; Zobel et al. 2011), there is a lack of knowledge with respect to geographical distribution, ecological status, floristic composition and diversity pattern of existing populations of *Juniperus turbinata* ssp. *canariensis* on Tenerife. This is of great conservation concern since these woodlands have been included in the list of priority habitats of the European Union (9560: Endemic forests of *Juniperus*, Montesinos et al. 2009). On Tenerife, this habitat has almost completely been destroyed over the last five centuries, and its current extension is 290 ha, whereas thermophilous woodlands, as a whole, occupy today 437 ha, 1.5 % of their original extension of about 29.700 ha (Del Arco et al. 2010). As a consequence of the immense loss of juniper woodlands on Tenerife, the local authorities (Cabildo Insular de Tenerife) launched a project in 2005, financed by the European Union (Project LIFE04/NAT/ES/000064), to restore Canarian juniper woodlands in the northwestern region of the island.

The present study is part of this project and focuses on the following objectives: (1) to evaluate the distribution of the last remnants of juniper woodlands on Tenerife in order to reconstruct the potential geographical range of Canarian juniper, (2) to obtain insights into the ecological and floristic characterization of the *J. turbinata* stands, (3) to identify patterns of species richness, with special interest in endemic species richness and alien species distribution, and (4) to provide information for conservation strategies as well as for future monitoring and restoration projects of this habitat of priority. In general, we hypothesized that richness and composition of native and endemic species is mainly related to climatic factors, i.e. to the differences between the more humid and colder northern slope and the drier and warmer southern slope of the island, whereas the distribution of alien species is more influenced by human activities on the landscape scale and certain land use types or infrastructures such as roads.

## Materials and methods

### Study area

The study was carried out on Tenerife, the largest and highest island of the Canarian Archipelago. The island's surface area is about 2,034 km$^2$ and the highest point is reached at 3,718 m asl. at the peak of the Teide volcano. Owing to the steep elevation gradient, the following five zonal ecosystems can be found from the coast to the peak of the Teide (Del Arco et al. 2006b): (1) coastal sub-desert scrub, an open shrub vegetation adapted to the subtropical, semi-arid climate and dominated by stem succulents of the genus *Euphorbia* and leaf succulents or sclerophyllous shrubs; (2) thermophilous forest, including juniper woodlands, the object of this study; (3) evergreen laurel forest growing on the north and northeastern sides of the island and formed by evergreen tree species belonging to genera such as *Laurus*, *Apollonias*, *Persea*, *Ilex*, *Prunus*; (4) Canary pine forest, exclusively made up of *Pinus canariensis,* and distributed above the laurel forest on the windward slope and above the thermophilous woodlands on the leeward slope; and (5) summit broom scrub restricted to areas above the timber line with common shrub species, such as *Spartocytisus supranubius, Descurainia bourgeauana* and *Pterocephalus lasiospermus*, adapted to low temperature in winter and warm, dry conditions in summer.

The Canarian juniper, *J. turbinata* ssp. *canariensis* (Guyot) Rivas-Mart et al., is currently considered an endemic tree of the Canarian and Madeiran archipelagos (Acebes et al. 2010), despite the ongoing debate about its taxonomical status (Adams et al. 2002). Adams et al. (2006) and Adams (2008) classified the Canarian juniper populations as *Juniperus phoenicea* var. *turbinata*, whereas Farjon (2005) grouped them within *Juniperus phoenicea* var. *phoenicea*. Adams et al. (2009) found differentiation in the leaf volatile oils of populations from Madeira and the Canary Islands compared to populations in Spain and Morocco, but they concluded that these differences did not justify the recognition of *J. phoenicea* subsp. *canariensis*.

Nowadays, this species is absent from the more arid eastern islands of Fuerteventura and Lanzarote (Acebes et al. 2010), where it has probably been eliminated by human activity over the last few centuries (Reyes-Betancort et al. 2001). Thermophilous forests would potentially grow at intermediate altitudes between 0–200 and 500 m a.s.l. on the windward slope and between 300–500 and 700–1100 m a.s.l. on the leeward slope of the islands

(Del Arco et al. 2006a; Fernández-Palacios et al. 2008). Canarian juniper woodlands are considered to constitute the most extended thermophilous woodland on the western Canary Islands (Del Arco et al. 2010). However, specific models predicting the potential distribution of this species do not yet exist.

Other communities belonging to this vegetation type are dominated by species such as *Pistacia atlantica*, *P. lentiscus*, *Olea cerasiformis*, *Phoenix canariensis*, *Retama rhodorhizoides* or *Heberdenia excelsa* (Fernández-Palacios et al. 2008; Nezadal and Welss 2009). The climate is Mediterranean with annual precipitation between 250 and 450 mm, mostly occurring in winter, and with average temperature between 15 and 19 °C, depending on aspect and elevation. The Canarian juniper is not very demanding with respect to soil conditions, since it is able to grow on poorly developed, stony soils. However, soils of juniper woodlands can substantially vary according to altitude and exposure to the dominant northeastern trade winds (von Gaisberg 2005).

Local studies have mainly focused on the floristic composition and geographical aspects of some thermophilous communities, including the juniper woodlands on Tenerife (Criado 1982; Santos and Fernández 1983; Rodríguez et al. 1990; Marrero et al. 1992; Luis et al. 2005). Detailed distribution maps of this species exist for the islands of El Hierro (von Gaisberg 2005) and Gran Canaria (González-Artiles 2006), but no attempt has ever been made to identify the geographical range and the ecological status of this species on Tenerife. In general, phytosociological characterizations and ecological differentiations were presented by Rivas-Martínez et al. (1993) and by Del Arco et al. (2006b), whereas Domínguez-Lozano et al. (2010) highlighted the richness of endemic species of this vegetation type.

On Tenerife, juniper forests have almost completely been destroyed over the last five centuries, since the potential zone of this vegetation type was the most favorable place for human settlements and agriculture (Del Arco et al. 2010). Furthermore, timber was used for many kinds of tools and for constructing houses (Rodríguez and Marrero 1991; Fernández-Palacios et al. 2008).

## Data collection

We searched for juniper patches within the potential area of the thermophilous woodlands on the island of Tenerife between 2006 and 2009 as part of the activities carried out within the LIFE project. In total, we sampled 108 sites where *J. turbinata* ssp. *canariensis* was present. We installed 10 m radius circular plots (area: 314 $m^2$) around selected adult juniper individuals, identified all perennial understory vascular plant species within these plots and visually estimated their cover. Since remnants of Canarian juniper woodlands on this island are usually represented by very small groups of individuals, we selected at least one adult individual to study its associated flora. Annual species were not recorded because it was not possible to sample sites twice a year in order to obtain a complete list of this species group. Furthermore, we were mainly interested in characterizing the understory shrub community for regeneration purposes. The percentage of annual species in this vegetation type varies considerably with the degree of human disturbance, structure and local climatic conditions. The highest participation of annuals, up to 50 % of the total species richness per plot, was found in substitution shrub communities within the potential area of humid juniper woodlands on the island of El Hierro (von Gaisberg 2005).

For each plot, we obtained UTM coordinates with a Global Positioning System device (model GPS, Garmin, Olathe, Kansas, USA), and several environmental and biotic variables were recorded in the field, such as altitude, slope inclination, slope aspect, cover of rocks and superficial soil, as well as total cover of trees, shrubs and perennial herbs. Cover values were visually estimated.

Climatic variables were interpolated applying spatial interpolation tools implemented in a Geographical Information System (GIS). After testing various interpolation techniques, we selected ordinary co-kriging (OCK) incorporating elevation from a Digital Elevation Model (DEM), since it provided the most accurate results after testing for prediction errors of cross-validation. The application of this geo-statistical approach is particularly justified in areas where landform is very complex (Diodato 2005). All the calculations were carried out using the Geostatistical Analyst module implemented in ArcGIS-ESRI software. Interpolation maps were elaborated with grid cell size of 50 × 50 m for several climatic variables provided by the Botany Department of La Laguna University.

Additionally, we extracted spatial information at a landscape scale by analyzing the surroundings of the plots and using spatial analysis tools incorporated in ArcGis. Areas of main land use types were calculated within a buffer of 500 m around the plots (area: 0.785 $km^2$) and nearest distances from plot center to land use or infrastructure types were analyzed (Table 1). Information on thematic layers was obtained from GRAFCAN S.L., Tenerife.

Plants were grouped, according to their status, into single island endemics (SIE), restricted to the island of Tenerife, Canarian endemics, Macaronesian endemics (endemic to the Canary Islands and Madeira), non-endemic natives and alien species. Recent checklists were used for classification (von Gaisberg 2005; Stierstorfer and von Gaisberg 2006; Acebes et al. 2010).

## Statistical analysis

We applied multivariate statistical techniques to analyze the influence of selected explanatory variables on species composition and richness of remnants of juniper woodlands. To avoid multi-colinearity effects in multiple regression analysis, a correlation matrix was constructed using non-parametric Spearman rank correlation coefficient to explore relationships among explanatory variables. We then selected a set of explanatory variables to enter in the regression analysis, by eliminating those variables that were highly correlated with each other ($r > 0.70$) and exhibited low tolerance statistics (<0.3) in ordinary least square regression analysis (OLS). In a second step, we used generalized additive models (GAM; Zuur et al. 2007) to evaluate the effect of each selected explanatory variable on species richness groups. This non-parametric model is especially recommended to detect non-linear relationships among variables. Since dependent variables and their error distributions were not normally distributed, species richness was finally analyzed applying generalized linear models (GLMs) with Poisson error distribution, using a log-link function, as recommended for count data in ecological analysis (Crawley 1993). In a GLM, the probability distributions of the dependent variable also include distributions of the exponential family such as a Poisson or binomial distribution (McCullagh and Nelder 1989; Dobson 1990). A link function provides the relationship between the linear predictor that incorporates the information of the independent variables and the mean of the distribution function. Predictor variables may be either numerical or categorical. Explanatory variables that showed uni-modal relationships in GAMs were included in GLMs with an additional quadratic term. To obtain the optimal set of predictor variables, we used AIC (Akaike Information Criteria) with forward stepwise selection, choosing the lowest AIC value for every possible combination of explanatory variables. Regression analyses were run using the software STATISTICA 8.

**Table 1** Results of basic statistics of all explanatory and dependent variables for all 108 plots studied, and differentiated between windward ($n = 46$) and leeward slope ($n = 62$) of the island of Tenerife

| Explanatory variables | Mean | Min. | Max. | Std. | Mean W | Mean L | *p* value |
|---|---|---|---|---|---|---|---|
| Altitude (m) | 505.3 | 10.0 | 1108.0 | 255.5 | 273.1 | 677.5 | <0.001* |
| Slope (°) | 35.5 | 0 | 75.0 | 14.60 | 32.5 | 39.2 | 0.016 |
| MAT (mm) | 17.2 | 14.3 | 19.5 | 1.4 | 18.2 | 16.5 | <0.001* |
| MAP (mm) | 383.4 | 194.3 | 610.1 | 131.7 | 476.1 | 313.7 | <0.001* |
| MSP (mm) | 14.1 | 3.9 | 37.3 | 7.5 | 19.0 | 10.4 | <0.001* |
| Soil cover (%) | 29.9 | 0 | 95.0 | 23.9 | 36.7 | 21.6 | <0.001* |
| Tree cover (%) | 27.6 | 0 | 75.0 | 19.4 | 33.1 | 21.0 | <0.001* |
| Shrub cover (%) | 38.6 | 5.0 | 90.0 | 21.3 | 39.0 | 38.1 | 0.824 |
| Herb cover (%) | 12.9 | 0 | 85.0 | 17.5 | 16.0 | 9.2 | 0.046 |
| Urbanized areas (ha) | 1.1 | 0 | 7.3 | 1.7 | 0.9 | 1.2 | 0.377 |
| Cultivated areas (ha) | 10.0 | 0 | 59.7 | 15.7 | 12.8 | 6.7 | 0.045 |
| Abandoned areas (ha) | 10.8 | 0 | 70.9 | 17.3 | 9.2 | 12.8 | 0.287 |
| Forests (ha) | 3.2 | 0 | 66.5 | 12.0 | 0.3 | 6.7 | 0.005 |
| Shrubland (ha) | 51.1 | 2.3 | 78.5 | 22.2 | 52.3 | 49.5 | 0.521 |
| Dist main road (km) | 0.7 | 0 | 2.3 | 0.58 | 738.6 | 543.4 | 0.080 |
| Dist cultivated areas (km) | 0.5 | 0 | 2.3 | 0.5 | 484.0 | 555.9 | 0.449 |
| Dist urbanized areas (km) | 1.0 | 0 | 3.0 | 0.8 | 1062.4 | 992.3 | 0.634 |
| Dist forests (km) | 1.4 | 0 | 3.5 | 1.0 | 1325.3 | 1571.1 | 0.188 |
| *Dependent variables* | | | | | | | |
| Total species richness | 21.3 | 10.0 | 42.0 | 6.4 | 20.8 | 21.8 | 0.401 |
| Endemic species | 15.6 | 5.0 | 34.0 | 5.3 | 15.5 | 15.8 | 0.832 |
| SIE | 1.9 | 0 | 6.0 | 1.3 | 2.1 | 1.7 | 0.138 |
| Native species | 4.4 | 0 | 10.0 | 2.0 | 3.9 | 4.9 | 0.009 |
| Alien species | 1.2 | 0 | 5.0 | 1.2 | 1.3 | 1.1 | 0.434 |
| Thermophilous species | 3.8 | 1.0 | 10.0 | 2.1 | 4.3 | 3.3 | 0.017 |

Differences of means between both slope types were tested applying non-parametric Kolmogorov–Smirnov test (*W* windward, *L* leeward, *p* value of *t*-test comparing windward and leeward slope, *Significant after Bonferroni corrections). *MAT* mean annual temperature, *MAP* mean annual precipitation, *MSP* mean summer precipitation (J, A, S), *land use types* area occupied (ha) within a buffer of 500 m around the juniper plot, *Dist* distance from plot centre to nearest land use type, *SIE* single island endemic species

Ordination techniques represent useful tools to explain variation in species composition of communities (Gauch 1982) and to evaluate major floristic gradients in time as well as in space (Ter Braak and Smilauer 1998). We chose the indirect gradient analysis based on Detrended Correspondence Analysis (DCA; Hill and Gauch 1980) of the software package CANOCO (Ter Braak and Smilauer 1998) to evaluate major floristic gradients and to examine how species composition was related to explanatory variables. We therefore extracted the coordinates of the first three DCA axes and correlated them against the explanatory variables using Spearman correlation coefficients. Additionally, we constructed Canonical Correspondence Analyses (CCAs) to confirm and visualize the results obtained from the correlation analysis. The classification of typical species for each ecosystem follows Zobel et al. (2011).

In order to floristically classify the juniper stands, we performed cluster analysis using a hierarchical, agglomerative cluster analysis on the samples with a relative Sørensen distance measure and a flexible beta of −0.25 (McCune and Grace 2002). Then, the optimal number of clusters was chosen using a MRPP (Multiple Response Permutation Procedures). This is a non-parametric multivariate test similar to a multivariate ANOVA, which can be used to compare results of different groups (McCune and Grace 2002). It was performed on data separated into at least two clusters and up to 17 clusters. We used Sørensen distances and PC-ORD default group weightings for all MRPP analyses (McCune and Grace 2002). Results from the MRPPs that showed high separation between groups (T-statistic) and high homogeneity within groups (A statistic) were used to select the best number of plot clusters (Dolan and Parker 2005). The more negative T is, the stronger the separation is between groups. A statistic ranges from −1 to 1, where 1 signifies that all objects are identical within groups (Chávez and Macdonald 2005). Even with significant separation of groups, A statistic values of less than 0.1 are common with community data (McCune and Grace 2002).

After the optimum number of clusters was determined, an indicator species analysis (ISA) was performed to identify which species were important to each cluster group. Indicator species analysis provides a method of combining the relative abundance and relative frequency of each species into an indicator value (Dufrêne and Legendre 1997). Indicator values were then tested for statistical significance using a randomization technique (Monte Carlo test) with 4,999 iterations. The randomizations were used to test the statistical significance of each species. The statistical software PC-Ord Version 6.0 (McCune and Mefford 2011) was applied for the vegetation classification.

## Results

### Habitat characterization

Patches of juniper woodlands were found within a circuminsular distribution with two major gaps, one between the Güímar Valley and the Anaga Mountains in the Northeast and another one between Anaga Mountains and the Orotava Valley in the North (Fig. 1). We found a significant difference in altitudinal distribution between windward (mean: 273 m, range: 10–580 m) and leeward slopes (mean: 678 m, range: 312–1108 m; Table 1; Fig. 2). Mean annual precipitation ranged from 200 to 600 mm, with a mean of 383 mm, while mean annual temperature ranged from 14 to 19.5 °C with an average of 17.2 °C. The juniper habitat was confirmed to be significantly drier and colder on the leeward compared to the windward slope. Furthermore, stands in the North of the island showed significantly higher soil and tree cover than those in the South. For the rest of habitat characteristics, we did not observe significant differences between slope types. In general, stands grow at present at sites with a considerable inclination, showing low tree and high shrub cover due to the degradation of the original vegetation. Consequently, shrubland dominated around the juniper stands (within an area of 0.785 $km^2$) followed by abandoned and cultivated areas. Main roads, urbanized and cultivated areas were, on average, not further than 1 km and never further than 3 km away from the stands studied, reflecting considerable landscape and habitat fragmentation.

### Richness pattern

Despite the clear signs of habitat fragmentation and degradation mentioned above, we still found a very high species richness, especially in endemic species, in the juniper stands

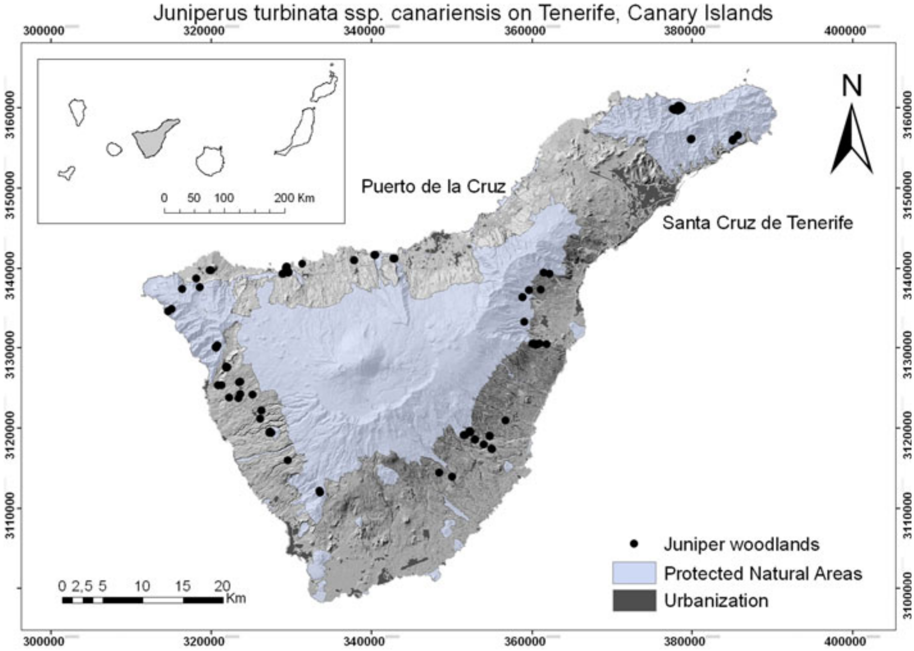

**Fig. 1** Location of the studied patches of *Juniperus turbinata* ssp. *canariensis* woodlands on Tenerife, Canary Islands

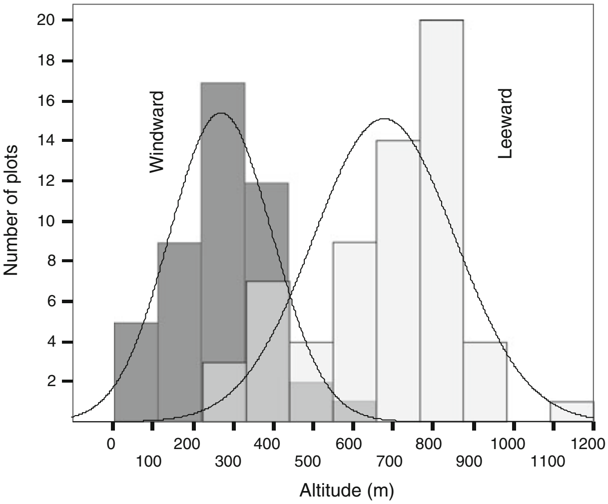

**Fig. 2** Altitudinal distribution of Canarian Juniper woodlands at the windward and leeward slope of Tenerife, Canary Islands (with Gaussian distribution model shown)

studied on Tenerife. In all plots, we recorded 214 perennial vascular plant species, out of these, 132 were Macaronesian endemics (62 %), 57 non-endemic native (26 %) and 25 alien species (12 %), while the entire perennial flora of the Canary Islands only exhibits a corresponding value of 43 % endemics (Acebes et al. 2010). With respect to the perennial flora of Tenerife, we detected 47 % of all endemic plants present on this island within the 108 plots, covering a total surface of only 34 ha.

The understory layer of this habitat harbored, on average, 15.6 endemic plants per plot (314 $m^2$) (73 % of the total average plot richness of 21.3) showing a maximum of 34 endemics (Table 1). Within this group, we detected 1.9 single island endemics per plot (max. 6 SIE). Thermophilous species showed a mean value of 3.8 and a maximum value of ten species per plot. The number of perennial alien species was quite low (1.2 on average, maximum 5), but one of them, *Opuntia maxima*, considered invasive in the Canary Islands, was found in 56 % of the stands with maximum cover values of 25 %. The most diverse juniper woodland patch, located on the southern slope of the Anaga mountains, was composed of five single island endemics, 24 Canarian endemics, five Macaronesian endemics and eight non-endemic native species.

The results of the correlation matrix showed some important correlations between explanatory variables, such as the correlation between altitude and mean annual temperature, altitude and slope type or the correlations between most of the land-use distance measurements with the corresponding surface measurements around the stands. Results of GAM showed an important uni-modal relationship between mean summer precipitation and most of the species groups studied. Therefore, a quadratic term for this variable in the regression analysis was also included.

Modeling species richness by means of GLMs revealed interesting insights into the existing richness pattern (Table 2). Herb and soil cover, as well as urbanized areas, around the plots had an overall negative effect on total species richness. Mean summer precipitation was observed to have a clear uni-modal relationship, showing higher richness values at intermediate precipitation levels. Richness of endemic species followed the same patterns. Regarding native species richness, we only obtained a weak negative linear relationship with mean annual precipitation. Richness of alien species was best predicted by herb cover at the plot scale and by the abundance of disturbed areas (areas of cultivated and urbanized land) at the landscape scale. The best predictor for the number of thermophilous species per plot was mean summer precipitation, revealing a uni-modal relationship. Additionally, tree cover had a positive effect on this species group. On the whole, deviance explained by the models was relatively low, indicating that there might be other important factors influencing richness pattern not included in this study.

## Species composition

Detrended Correspondence Analysis indicated that slope orientation was by far the strongest factor influencing plant species composition of juniper stands on Tenerife. Species with highest abundance on the windward slope are located on the right side of the DCA diagram, species common on the leeward slope on the opposite side (Fig. 3). Slope orientation was strongly correlated with the sample scores of the first DCA axis (Table 3). Lower, but still significant correlation coefficients were shown by altitude and all the climatic variables. Overall, the first DCA axis was related to a climatic gradient separating more humid and warmer windward sites from drier and colder leeward sites. The length of the gradient of the first DCA axis reached 3.6 SD, indicating high $\beta$-diversity and an almost full species turnover, which occurs at four SD units (Gauch 1982).

The highest correlation coefficients with the coordinates of the second DCA axis were shown by the tree and herb cover variables, separating closed from rather open juniper

**Table 2** Results of generalized linear models (GLMs) for all 108 plots studied, showing the best set of explanatory variables explaining richness of different species groups as response variable, using AIC (Akaike Information Criteria) best set selection and Poisson distribution with log-link function (*MAP* mean annual precipitation, *MSP* mean summer precipitation, *Dev. expl.* deviance explained)

| Species group | Parameter estimates | | | Model building results | | |
|---|---|---|---|---|---|---|
| | Estimate | Wald's $\chi^2$ | *p* value | AIC | *p* value | Dev. expl. |
| Total richness | | | | | | |
| Intercept | 2.9061 | 1211.14 | <0.001 | 671.8 | <0.001 | 36.2 |
| Herb cover | −0.0087 | 31.29 | <0.001 | | | |
| MSP | 0.0458 | 16.97 | <0.001 | | | |
| MSP × MSP | −0.0012 | 12.26 | <0.001 | | | |
| Soil cover | −0.0027 | 6.51 | 0.011 | | | |
| Urbanized areas | −0.0001 | 5.56 | 0.018 | | | |
| Endemic species | | | | | | |
| Intercept | 2.5804 | 714.16 | <0.001 | 608.3 | <0.001 | 39.8 |
| Herb cover | −0.0082 | 21.93 | <0.001 | | | |
| MSP | 0.0529 | 17.02 | <0.001 | | | |
| MSP × MSP | −0.0013 | 11.84 | 0.001 | | | |
| Soil cover | −0.0030 | 6.05 | 0.014 | | | |
| Urbanized areas | −0.0004 | 5.90 | 0.015 | | | |
| Native species | | | | | | |
| Intercept | 1.6422 | 119.74 | <0.001 | | | 14.6 |
| MAP | −0.0008 | 4.21 | 0.040 | | | |
| Alien species | | | | | | |
| Intercept | −2.5481 | 4.01 | 0.045 | 318.2 | <0.001 | 15.6 |
| Herb cover | −0.0240 | 7.67 | 0.006 | | | |
| Disturbed areas | 0.0001 | 6.64 | 0.010 | | | |
| Thermophilous species | | | | | | |
| Intercept | 0.4096 | 3.78 | 0.049 | 421.7 | <0.001 | 26.4 |
| MSP | 0.1078 | 12.41 | 0.000 | | | |
| MSP × MSP | −0.0031 | 10.75 | 0.001 | | | |
| Tree cover | 0.0074 | 7.51 | 0.006 | | | |

stands. Mean annual temperature was a less important factor correlated with this axis that, overall, revealed structural differences of the vegetation. The third DCA axis was clearly related to land use types and the degree of landscape transformation since the cultivated and urbanized area variables, as well as most of the land-use distance measurements, were correlated with the scores of this axis.

The species scatter plot of the two first DCA axes (Fig. 3) clearly displays the vegetation belts of Tenerife in contact with the juniper woodlands, with the typical species of each habitat represented by their centroids. On the northern slope, we can find remnants of thermophilous woodlands from the coast up to 200–500 m, where the transition to laurel forest occurs (right side of the figure). In the South of the island (left in the figure), juniper stands are mixed with succulent scrub formed mainly by *Euphorbia* species at low altitudes and with pine forest species at higher altitudes, indicating the transition from juniper woodlands to Canary Island pine forest. In one location, in the Güímar Valley, in the

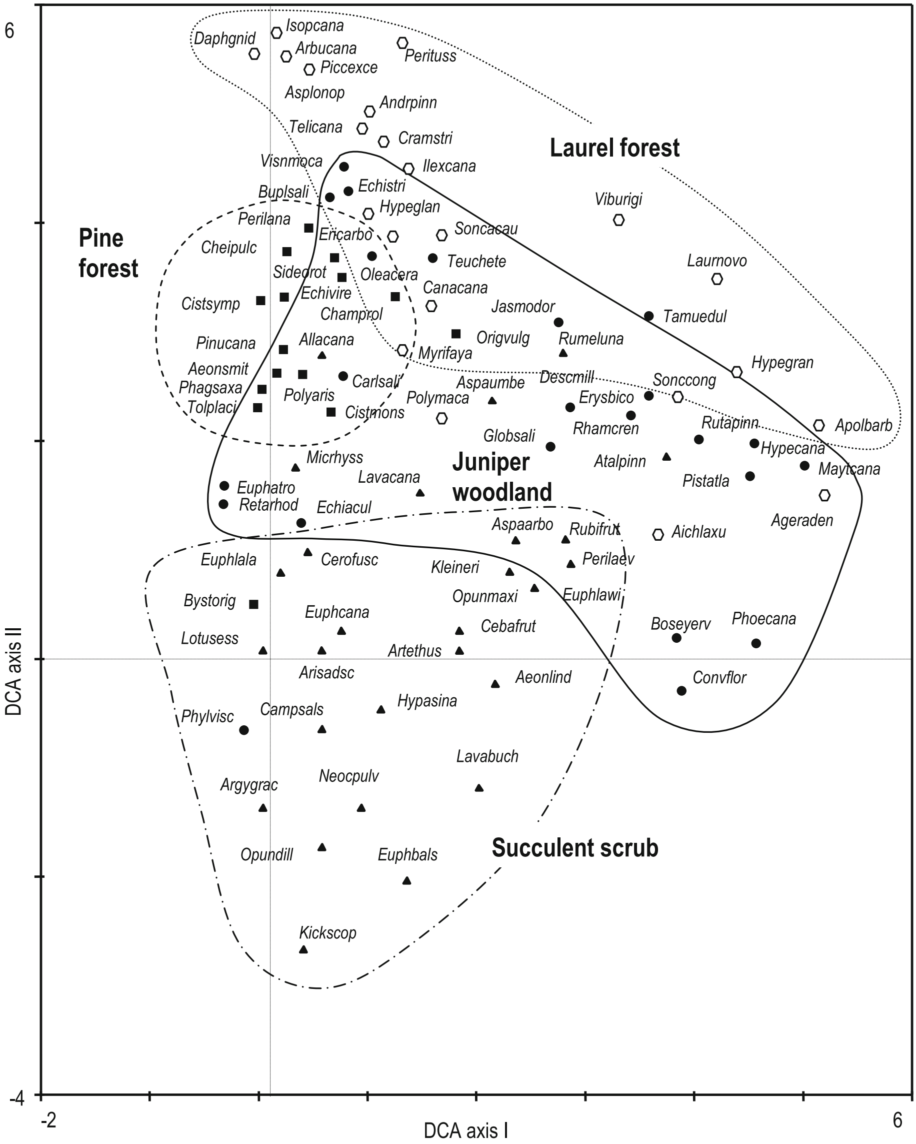

**Fig. 3** DCA ordination diagram of the first two axes displaying centroids of typical species found in 108 juniper woodland patches on the island of Tenerife. The eigenvalues of the axes were 0.436 and 0.310, the cumulative percentage variance of species data of the first two axes reached 14.5 %. Square root transformation of species cover values and down weighting of rare species were selected as options of analysis (*circles* thermophilous species, *triangles* succulent scrub species, *squares* pine forest species, *open hexagons* laurel forest species, abbreviation of species: first four letters of genus name and first four letters of species name, see "Appendix")

Southeast of the island, laurel forest, pine forest and thermophilous woodland species coexist. CCA ordination confirmed the relationship between climatic variables with the first axis, structural variables (tree and herb cover) with the second axis and human disturbance with the third axis (Fig. 4).

**Table 3** Spearman coefficients of correlations between explanatory variables and coordinates of the first three DCA axes (abbreviations see table 1)

| Explanatory variables | DCA_axis 1 | DCA_axis 2 | DCA_axis 3 |
|---|---|---|---|
| Altitude | −0.699 | 0.237 | 0.217 |
| Windward/Leeward | 0.851 | −0.105 | −0.124 |
| UTM X | 0.361 | 0.236 | 0.201 |
| UTM Y | 0.786 | −0.035 | 0.115 |
| Slope inclination | −0.218 | 0.325 | 0.103 |
| MAT | 0.518 | −0.344 | −0.267 |
| MAP | 0.561 | 0.176 | 0.205 |
| MSP | 0.561 | 0.176 | 0.205 |
| Soil cover | 0.366 | 0.083 | −0.063 |
| Tree cover | 0.296 | 0.406 | −0.044 |
| Shrub cover | 0.045 | −0.042 | −0.283 |
| Herb cover | 0.164 | −0.411 | 0.371 |
| Urbanized areas | 0.084 | −0.136 | −0.394 |
| Cultivated areas | 0.288 | 0.115 | −0.568 |
| Abandoned areas | −0.206 | 0.034 | −0.183 |
| Forests | −0.121 | 0.052 | 0.322 |
| Shrubland | −0.010 | −0.196 | 0.459 |
| Dist main road | 0.047 | −0.004 | 0.457 |
| Dist cultivated areas | −0.203 | −0.129 | 0.547 |
| Dist urbanized areas | 0.012 | 0.115 | 0.495 |
| Dist forests | −0.289 | −0.180 | −0.378 |

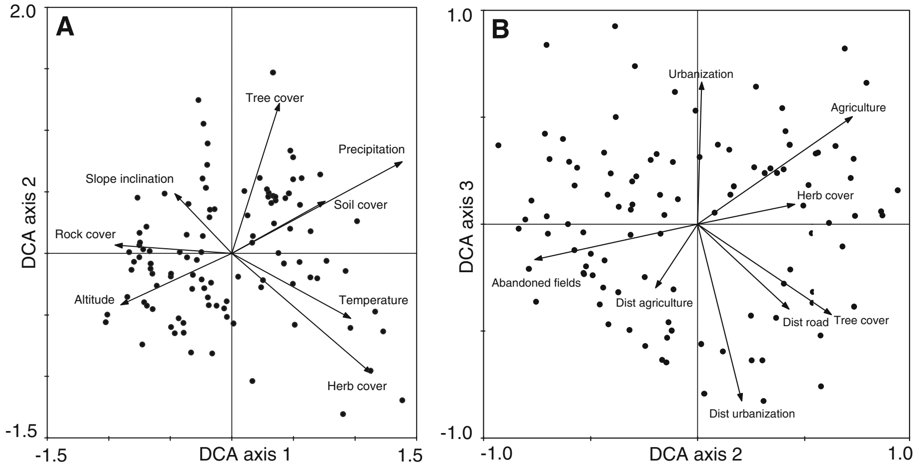

**Fig. 4** CCA ordination diagrams showing biplots of significant explanatory variables and 108 sites of juniper woodland patches on the island of Tenerife. **a** Ordination representing the first and second axis of the CCA and **b** Second and third CCA axis. The eigenvalues of the axes were **a** 0.242 and 0.203, and **b** 0.230 and 0.197. Square root transformation of species cover values and down weighting of rare species were selected as CCA options (*dist* distance from plot centre to nearest land use type)

### Vegetation classification

The MRPP indicated that the optimal number of clusters was between six and eight sample groups. We chose a classification with eight clusters, since it provided the optimal combination of low T-statistic and high A-value ($T = -38.4$; $A = 0.185$). The indicator species analysis identified 36 species, only considering species with $p$ values $<0.1$, out of 214 as significant indicators of one of the eight juniper woodland types (Table 4). Two groups (G1 and G8) were characterized by the combination of locally abundant endemic shrubs. The first type showed high cover values of *Euphorbia atropurpurea*, *R. rhodorhizoides*, *Phagnalon purpurascens* and *Echium aculeatum* and was located in the Southwest of the island at relatively high altitudes compared to the mean values of the other groups (Table 5). The first two species were not selected by ISA, but showed the highest cover values in this rather species poor type, also characterized by the highest herb cover and a low shrub cover. Type G8 represents a variant in the Anaga Mountains in the northeastern part of Tenerife, where local endemics such as *Aeonium lindleyi* frequently grow at lower altitudes. The juniper patches of this type exhibited high herb and shrub cover and low species richness. The only indicator species of group G2 was *Euphorbia lamarckii* ssp. *lamarckii*, an endemic spurge growing mainly in the South of the island. Analyzing the whole floristic composition of this type, we also detected high abundances of shrubs, such as *Cistus monspeliensis* and *Artemisia thuscula*, although these species did not reach significant indicator species values, since they are also present in lower abundances in other groups.

Two single island endemic shrubs, *Pericallis lanata* and *Echium virescens*, were selected as indicator species of type G3, which was characterized by the highest values of total species richness and pine forest species richness, as well as by low tree, herb and soil cover. Type G4 included *P. canariensis* as an indicator species and clearly represented a transition from juniper woodlands to pine forest, including in some cases *Erica arborea*. Laurel forest tree species, such as *Ilex canariensis* and *Visnea mocanera,* and the thermophilous tree *O. cerasiformis* were indicators of type G5, growing mainly on the northern slope of the island and showing the highest participation of laurel forest and thermophilous species as well as the highest tree cover among all the different types. Endemic shrub species present in the northern part of the island, such as *Sonchus congestus*, *Echium giganteum* and *Atalanthus pinnatus,* were typical of group G6 that exhibited highest shrub and soil cover. Juniper patches of group G7 had ten indicator species, all of them typical of succulent scrub growing at low altitudes in the dry South of the island. Herb and tree cover was low in this type.

## Discussion

### Species richness

The Canarian Archipelago, biogeographically included in the Mediterranean Basin (Blondel and Aronson 1999), is considered one of the most important biodiversity hotspots in the world (Médail and Quézel 1997) due to the high level of endemism of its biota (Whittaker and Fernández-Palacios 2007). Within the Canarian Archipelago, Tenerife is the most diverse island with respect to the number of habitats and endemic plants because of its altitude, age and size (Fernández-Palacios and de Nicolás 1995; Zobel et al. 2011). Recent studies analyzing species pools of vascular plants at the habitat level on the Canary

**Table 4** Results of the Indicator Species Analysis for the (8 or eight) juniper woodland types (or groups) identified by means of a Multi-response Permutation Procedure (MPPP) after a cluster analysis

| Juniper woodland type/species | Indicator value | *p* value |
|---|---|---|
| G1 *Euphorbia atropurpurea*-Type | | |
| *Umbilicus horizontalis* | 75 | 0.001 |
| *Phagnalon purpurascens* | 74 | 0.001 |
| *Echium aculeatum* | 68 | 0.001 |
| *Gonospermum fruticosum* | 62 | 0.001 |
| *Lobularia canariensis* | 56 | 0.001 |
| G2 *Cistus-Artemisia*-Type | | |
| *Euphorbia lamarckii* | 11 | 0.082 |
| G3 *Pericallis lanata*-Type | | |
| *Pericallis lanata* | 32 | 0.013 |
| *Echium virescens* | 24 | 0.028 |
| *Monanthes brachycaulos* | 23 | 0.028 |
| *Tolpis laciniata* | 18 | 0.072 |
| G4 *Pinus-Erica*-Type | | |
| *Pinus canariensis* | 23 | 0.051 |
| *Bituminaria bituminosa* | 42 | 0.012 |
| *Paronychia canariensis* | 25 | 0.021 |
| *Descurainia millefolia* | 22 | 0.043 |
| G5 *Ilex canariensis*-Type | | |
| *Ilex canariensis* | 15 | 0.100 |
| *Olea cerasiformis* | 27 | 0.012 |
| *Visnea mocanera* | 20 | 0.050 |
| *Bystropogon canariensis* | 16 | 0.050 |
| G6 *Sonchus congestus*-Type | | |
| *Sonchus congestus* | 49 | 0.001 |
| *Atalanthus pinnatus* | 41 | 0.004 |
| *Echium giganteum* | 40 | 0.001 |
| *Asparagus umbellatus* | 37 | 0.008 |
| *Aeonium canariense* | 36 | 0.006 |
| *Bystropogon origanifolius* | 36 | 0.002 |
| G7 *Euphorbia balsamifera*-Type | | |
| *Euphorbia balsamifera* | 40 | 0.001 |
| *Euphorbia canariensis* | 36 | 0.005 |
| *Lavandula buchii* | 56 | 0.001 |
| *Cenchrus ciliaris* | 50 | 0.001 |
| *Drimia maritima* | 46 | 0.001 |
| *Kleinia neriifolia* | 43 | 0.001 |
| *Kickxia scoparia* | 42 | 0.001 |
| *Neochamaelea pulverulenta* | 33 | 0.008 |
| *Ceballosia fruticosa* | 25 | 0.026 |
| *Campylanthus salsoloides* | 20 | 0.033 |
| G8 *Aeonium lindleyi*-Type | | |
| *Aeonium lindleyi* | 85 | 0.001 |
| *Plantago arborescens* | 59 | 0.001 |

**Table 5** Mean richness values of typical habitat species and some structural characteristics for the classified juniper woodland types

| Characteristics | G1 | G2 | G3 | G4 | G5 | G6 | G7 | G8 |
|---|---|---|---|---|---|---|---|---|
| *Thermophilous* sp. | 4.8 | 3.8 | 3.1 | 4.5 | 5.4 | 4.7 | 3.6 | 2.4 |
| Succulent scrub species | 8.6 | 9.5 | 12.3 | 6.2 | 8.5 | 10.3 | 14.6 | 6.5 |
| Laurel forest species | 1.2 | 1.1 | 1.4 | 3.5 | 5.0 | 1.7 | 1.0 | 1.0 |
| Pine forest species | 1.2 | 2.6 | 5.5 | 4 | 1.9 | 1.2 | 1.5 | 0.9 |
| Total richness | 15.8 | 17.0 | 22.3 | 18.2 | 20.8 | 17.9 | 21.7 | 10.8 |
| Altitude (m) | 660.0 | 708.0 | 569.0 | 676 | 403.0 | 398.0 | 390.0 | 282.0 |
| Tree cover (%) | 30.0 | 21.1 | 14.2 | 22.8 | 38.8 | 23.5 | 11.3 | 14.5 |
| Shrub cover (%) | 25.0 | 45.3 | 26.6 | 21.7 | 38.7 | 51.7 | 38.2 | 44.5 |
| Herb cover (%) | 49.0 | 10.7 | 2.8 | 14.1 | 4.1 | 18.5 | 6.5 | 46.0 |
| Soil cover (%) | 20.4 | 18.1 | 15.7 | 21.5 | 40.7 | 48.3 | 28.6 | 41.0 |

Islands revealed that thermophilous woodlands, including juniper woodlands, together with the summit scrub showed the highest levels of diversity of endemic species (Domínguez-Lozano et al. 2010; Zobel et al. 2011; Steinbauer et al. 2011).

The present study carried out at the level of plot or α-richness confirmed the outstanding diversity of perennial vascular plants, especially of endemics, of the last remnants of juniper woodlands on Tenerife. Although there is a lack of comparative studies of richness patterns using the same plot size for all main ecosystems of the island, we can show that the remaining juniper woodland patches represent high local biodiversity spots within the recognized regional biodiversity hotspot of the Canarian Archipelago. With respect to perennial vascular plants, and depending on plot size (100–400 $m^2$), mean richness values per plot of 12–19 species were recorded for the succulent scrub, 21.3 for juniper woodlands (present study), 10–15 for the laurel forest, 4–8 for the pine forest and 3–6 for the summit scrub (Fernández-Palacios 1987; Otto et al. 2001; Otto 2003; Otto et al. 2010). This would indicate a hump-shaped distribution of habitat richness along the elevation gradient on Tenerife with maximum richness at mid-altitudes, i.e. within the potential area of thermophilous woodlands and lower laurel forests. Similar patterns have been reported in other regions of the world and on islands (McCain 2007; Jakobs et al. 2010). Several explanations have been put forward for this pattern such as the mid-domain effect caused by overlapping altitudinal species ranges (Rahbek 1995), decreasing area effect with increasing elevation (Körner 2007) or water-energy-availability (O’Brien et al. 2000; Currie et al. 2004; McCain 2007).

Modeling within habitat richness patterns by applying GLMs, we found that overall richness, richness of endemic species and the number of thermophilous species recorded in juniper patches were best predicted by mean summer rainfall showing a uni-modal relationship. This observation might be explained by the water-energy-hypothesis (Rosenzweig and Abramsky 1993), since the drier, lower part of the island within the habitat of succulent scrub perennial plant richness was found to positively correlate with mean annual precipitation (Otto et al. 2001). The positive correlation of richness with precipitation at juniper sites with low and intermediate water availability would represent the continuation of this trend. On the other hand, structural vegetation changes could be responsible for the slight decrease of richness in juniper patches at sites with higher water availability in the transition zone to laurel and pine forest, where increasing tree cover possibly limits understory plant richness due to competition for light. A similar hump-shaped richness pattern has been reported for roadside plant communities along the principal elevation gradient on Tenerife (Arévalo et al. 2005). The fact that thermophilous woodland species richness was not predicted by temperature seems to indicate that precipitation, i.e. mean summer precipitation, is limiting the distribution of this habitat at lower altitudes. This is consistent with the findings that compared to the windward slope, juniper stands grow at higher and colder sites in the South of the island where water availability is sufficient.

The increase of richness of native, non-endemic species with decreasing mean annual precipitation in the studied juniper woodlands can be explained by the increasing participation of succulent scrub species in the drier South of the island and their floristic relationship with shrub communities in northern Africa (Otto et al. 2001). Some typical species of the succulent scrub (*Euphorbia balsamifera*, *Launaea arborescens*, *Lycium intricatum,* etc.) are not endemic but shared with similar communities in Northwest Africa.

The strong negative effect of plot herb cover on richness of both endemic and alien perennial plants in juniper patches is probably related to human disturbance. Herb cover here is mainly formed by perennial grasses, which clearly indicate the influence of grazing and agricultural activities in the past, in the form of abandoned fields. Sites with high grass cover (>30 %) are strongly degraded and support lower number of shrub species independent of origin.

The degree of human activity within the landscape, here represented by the area of urbanized and agricultural land in the surroundings of the juniper patches, had a weak negative effect on richness of endemic species but a positive effect on the number of perennial alien species. In contrast to this negative relationship, a positive correlation between alien and endemic species was found in roadside communities along an elevation gradient on Tenerife (Arévalo et al. 2005). However, annuals were also included in the latter study, a species group that comprised the highest proportion of the alien flora of the Canary Islands. Therefore, the interpretation of our findings is limited in this context.

Our results show that perennial alien plants are rather scarce in the juniper woodlands but one invasive species, *Opuntia maxima*, frequently grows in this habitat with intermediate cover values, where it clearly competes with many endemic species, including the Canarian juniper. This noncolumnar cactus was introduced from Mexico to the Canary Islands in the sixteenth century for cultivation of fruits, fencing and the production of a red dye that was elaborated from the infesting cochineal insect *Dactylopius coccus*. As in other regions with Mediterranean climate (Vilà et al. 2003; Erre et al. 2009), *O. maxima* has rapidly spread into not only human disturbed areas, such as abandoned fields, but also semi-natural shrublands in the lower parts of all the Canary Islands due to the very successful recruitment by seedlings and cladodes and the positive interaction with native dispersers (Gimeno and Vilà 2002; Padrón et al. 2011). Cover of *O. maxima* in Canarian juniper woodlands was weakly negatively correlated (Pearson coefficient: 0.33, $p = 0.017$) with the distance to urban nuclei, which highlights the importance of landscape transformation in understanding the distribution and spread of this species (Vilà et al. 2003).

Overall, our results fit with the general findings that human disturbance is a strong driver of alien species richness and determines the invasion process on oceanic islands, which has been observed not only at island level (Denslow et al. 2009; Jakobs et al. 2010; Kueffer et al. 2010), but also at landscape and habitat level (Pretto et al. 2010). The importance of distance to nearest urban nuclei for alien plant richness in roadside communities has already been reported on the Canary Islands (Arévalo et al. 2005; Arteaga et al. 2009).

The most detailed study on *J. turbinata* ssp. *canariensis* has so far been carried out on the island of El Hierro (von Gaisberg 2005), where a negative correlation between canopy cover and understory plant richness of juniper stands was reported. Although canopy cover of some of our plots reached 85 %, we did not detect any correlations between this structural variable and plant richness. However, we cannot reject the hypothesis that the very high diversity of endemic species in the understory vegetation is partly related to the degradation of the tree layer and the subsequent colonization of endemic shrubs typical of substitution communities. Nevertheless, except when considering the transitional zones to forests, the habitat of the Canarian juniper is expected to be a rather open woodland with participation of many shrub species (von Gaisberg 2005). Decrease of understory plant diversity with increasing tree cover has been observed for other juniper woodlands (Miller et al. 2000).

## Species composition

In contrast to the richness patterns, DCA and cluster analyses revealed that the climatic differences between windward and leeward slope of the island had the strongest influence on plant species composition within the habitat of juniper woodlands. The effect of the exposure to the humid northeastern trade winds has already been highlighted for the whole island of Tenerife (Fernández-Palacios and de Nicolás 1995), as well as for a single habitat, the pine forest (Rivas-Martínez et al. 1993). Here, we can also confirm this pattern for the juniper woodlands on Tenerife, since the whole distribution range of this species that potentially rings the island was covered (Del Arco et al. 2006a). Furthermore, the contact of the studied habitat with three zonal ecosystems present on the Canary Islands, laurel forest, pine forest and succulent scrub, can be confirmed.

On the windward slope and at altitudes of 300–500 m a.s.l., we observed that laurel forest species usually participate in the formation of humid juniper woodland, which is here represented by cluster groups G5 and G6. The second one can be considered a degraded variant of the more conserved first type with higher species richness. The selected indicator species of type G5, as well as its high tree and soil cover, confirm the transition character between juniper woodland and laurel forest. A similar formation has been reported from the island of El Hierro (von Gaisberg 2005). Juniper patches at altitudes of 500–600 m on the windward slope of Tenerife are usually found on steep rocky slopes, since this zone, where more developed soils are available, would potentially already belong to the laurel forest. On the other hand, *J. turbinata* ssp. *canariensis* can grow close to the coast at favorable sites in the North of the Western Canary Islands (von Gaisberg 2005; Del Arco et al. 2006a; Fernández-Palacios et al. 2008).

In the South of Tenerife, the Canarian juniper has a wide altitudinal distribution range (300–1100 m), and some isolated individuals have even been found in the Teide crater of Las Cañadas at more than 2,000 m (Sventenius 1946). In lower regions, juniper stands are mixed with the succulent scrub: a vegetation type that is highly adapted to hydric stress almost over the whole year (Otto et al. 2001; Otto 2003). This habitat transition is represented by cluster group G7 and many indicator species. At the upper limit of the southern distribution range, juniper patches with participation of pine forest species were found. The exact location of this transitional zone from juniper woodlands to pine forest depends not only on local climatic conditions but also on the substrate type, since pine forest has been found to descend to the coast on salic lava flows in the SW and SE sector of the island (Del Arco et al. 2006b). Cluster groups G3 and G4 represented this influence of pine forest. Finally, cluster type G2 included strongly degraded juniper stands at intermediate and higher elevations on both slopes, characterized by high abundances of substitution shrub species such as *Euphorbia lamarckii*, *Cistus monspeliensis* and *Artemisia thuscula*.

In general, the last remnants of juniper woodlands on Tenerife have been found to exhibit both an extraordinary plant diversity at the plot level, i.e. high $\alpha$-diversity, especially of endemic plants and a high floristic variation within the island, i.e. high species turnover between sites or high $\beta$-diversity. Both of these findings are related firstly to climatic conditions, the result of the steep environmental gradients typical for most of the Canary Islands, and secondly to human disturbance and corresponding structural changes of the vegetation. The effect of landscape transformation by humans on species composition has also been reported for other *Juniperus* species (Milios et al. 2007).

Although two major distribution gaps of the Canarian juniper on Tenerife currently exist, coinciding with the most populated areas around the capital Santa Cruz and between the cities of La Laguna and Puerto de la Cruz, ecological characterization supported the idea that the habitat would potentially be circuminsular.

## Consequences for conservation

The closeness of all juniper patches to intensive human activities (agriculture, urbanizations, road constructions), the scattered distribution of the last remnants over the island and the very low number of juniper patches with more than 100 individuals confirmed not only the immense destruction and degradation of the original vegetation and the heavy landscape transformation at mid-altitudes of Tenerife, the so called "medianías" (Fernández-Palacios et al. 2008; Del Arco et al. 2010), but also demonstrated that this habitat is obviously threatened on Tenerife. Given the exceptional plant diversity of this habitat, a priority at European level, and the fact that 39 % of the studied juniper patches are not included in protected natural areas (Martín-Esquivel et al. 1995), the priority for conservation should be the immediate protection of all the remnants of juniper woodlands on the island of Tenerife. This is also justified by the findings that *J. turbinata* ssp. *canariensis* has a low regeneration capacity on this island due to low growth rates, dispersal difficulties and regeneration niches that depend on favorable environmental conditions and structural characteristics of the vegetation (Fernández-Palacios et al. 2008; Otto et al. 2010). In most of the juniper patches studied in the drier South of the island, no regeneration of the Canarian juniper and rarely fruit production have been observed (Otto and Barone, unpubl. data.). Considering that global climate change will also affect Tenerife by increasing temperatures (Martín-Esquivel et al. 2012), many of the juniper stands at lower altitudes in the South of the island will probably disappear in the future due to increasing environmental stress and lack of regeneration causing a local loss of biodiversity, including the loss of genetic diversity of these populations (Terrab et al. 2008).

After protecting the remaining juniper patches, eradication of the aggressive invader *Opuntia maxima* should be considered. Since this habitat revealed the highest degree of destruction and alteration of all major zonal ecosystems of the Canary Islands (Del Arco et al. 2010), restoration activities are urgently needed and should have priority in conservation plans. Considering that the highest diversity of juniper patches in endemic and thermophilous species are expected where water availability is higher, restoration projects would have best success on the more humid windward slope and probably also in the upper parts of the Güímar Valley in the Southeast of the island.

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## Appendix

Table 6.

**Table 6** List of species included in Fig. 3

| Species | Status |
|---|---|
| *Aeonium Lindley* | SIE |
| *Aeonium smithii* | SIE |
| *Ageratina adenophora* | ALI |
| *Aichryson laxum* | CAN |
| *Allagopappus canariensis* | CAN |
| *Andryala pinnatifida* | CAN |
| *Apollonias barbujana* | MAC |
| *Arbutus canariensis* | CAN |
| *Argyranthemum gracile* | SIE |
| *Aristida adscensionis* | NAT |
| *Artemisia thuscula* | CAN |
| *Asparagus arborescens* | CAN |
| *Asparagus umbellatus* | MAC |
| *Asplenium onopteris* | NAT |
| *Atalanthus pinnatus* | CAN |
| *Bosea yervamora* | CAN |
| *Bupleurum salicifolium* | MAC |
| *Bystropogon origanifolius* | CAN |
| *Campylanthus salsoloides* | CAN |
| *Canarina canariensis* | CAN |
| *Carlina salicifolia* | MAC |
| *Ceballosia fruticosa* | CAN |
| *Ceropegia fusca* | CAN |
| *Chamaecytisus proliferus* | CAN |
| *Cheilanthes pulchella* | NAT |
| *Cistus monspeliensis* | NAT |
| *Cistus symphytifolius* | CAN |
| *Convolvulus floridus* | CAN |
| *Crambe strigosa* | CAN |
| *Daphne gnidium* | NAT |
| *Descurainia millefolia* | CAN |
| *Echium aculeatum* | CAN |
| *Echium strictum* | CAN |
| *Echium virescens* | SIE |
| *Erica arborea* | NAT |
| *Erysimum bicolor* | MAC |
| *Euphorbia atropurpurea* | SIE |
| *Euphorbia balsamifera* | NAT |
| *Euphorbia canariensis* | CAN |
| *Euphorbia lamarckii* ssp. *lamarckii* | SIE |

**Table 6** continued

| Species | Status |
|---|---|
| *Euphorbia lamarckii* ssp. *wildpretii* | CAN |
| *Globularia salicina* | MAC |
| *Hyparrhenia sinaica* | NAT |
| *Hypericum glandulosum* | MAC |
| *Hypericum grandifolium* | MAC |
| *Ilex canariensis* | MAC |
| *Isoplexis canariensis* | CAN |
| *Jasminum odoratissimum* | MAC |
| *Kickxia scoparia* | CAN |
| *Kleinia neriifolia* | CAN |
| *Laurus novocanariensis* | NAT |
| *Lavandula buchii* | SIE |
| *Lavandula canariensis* | CAN |
| *Lotus sessilifolius* | CAN |
| *Maytenus canariensis* | CAN |
| *Myrica faya* | NAT |
| *Neochamaelea pulverulenta* | CAN |
| *Olea cerasiformis* | CAN |
| *Opuntia dillenii* | ALI |
| *Opuntia maxima* | ALI |
| *Origanum vulgare* | NAT |
| *Pericallis lanata* | SIE |
| *Pericallis tussilaginis* | CAN |
| *Periploca laevigata* | MAC |
| *Phagnalon saxatile* | MAC |
| *Phoenix canariensis* | CAN |
| *Phyllis viscosa* | CAN |
| *Picconia excelsa* | MAC |
| *Pinus canariensis* | CAN |
| *Pistacia atlantica* | NAT |
| *Polycarpaea aristata* | CAN |
| *Polypodium macaronesicum* | NAT |
| *Retama rhodorhizoides* | CAN |
| *Rhamnus crenulata* | CAN |
| *Rubia fruticosa* | MAC |
| *Rumex lunaria* | CAN |
| *Ruta pinnata* | CAN |
| *Sideritis oroteneriffae* | SIE |
| *Sonchus acaulis* | CAN |
| *Sonchus congestus* | CAN |
| *Tamus edulis* | MAC |
| *Teline canariensis* | CAN |
| *Teucrium heterophyllum* | MAC |

**Table 6** continued

| Species | Status |
|---|---|
| *Tolpis laciniata* | CAN |
| *Viburnum rigidum* | CAN |
| *Visnea mocanera* | MAC |

*SIE* Single island endemic, *CAN* Canary endemic, *MAC* Macaronesian endemic, *NAT* native non-endemic, *ALI* alien

## References

Acebes JR, León MC, Rodríguez ML, Del Arco MJ, García-Gallo A, Pérez-de-Paz PL, Rodríguez-Delgado O, Martín VE, Wildpret W (2010) Pteridophyta, spermatophyta. In: Arechavaleta M, Rodríguez S, Zurita N, García A (eds) Lista de especies silvestres de Canarias. Hongos plantas y animales terrestres. Gobierno de Canarias, Tenerife, pp 119–172

Adams RP (2008) Junipers of the world: the genus *Juniperus*, 2nd edn. Trafford Publication, Vancouver

Adams RP, Pandey RN, Rezzi S, Casanova J (2002) Geographic variation in the Random Amplified Polymorphic DNAs (RAPDs) of *Juniperus phoenicea*, *J. p.* var. *canariensis*, *J. p.* subsp. *eumediterranea*, and *J. p.* var. *turbinata*. Biochem Syst Ecol 30:223–229

Adams RP, Nguyen S, Achak N (2006) Geographic variation in *Juniperus phoenicea* (Cupressaceae) from the Canary Islands, Morocco and Spain based on RAPDs analysis. Phytologia 88(3):270–278

Adams RP, Rumeu B, Nogales M, Fontinha S (2009) Geographic variation and systematics of *Juniperus phoenicea* l. from Madeira and the Canary islands: analyses of leaf volatile oils. Phytologia 91(1):39–52

Arévalo JR, Delgado JD, Otto R, Naranjo A, Salas M, Fernandez-Palacios JM (2005) Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspect Plant Ecol Evol Syst 7:185–202

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

Arteaga MA, Delgado JD, Otto R, Fernandez-Palacios JM, Arévalo JR (2009) How do alien plants distribute along roads on oceanic islands? A case study in Tenerife, Canary Islands. Biol Invasions 11:1071–1086

Bacaro G, Santi E, Rocchini D, Pezzo F, Puglisi L, Chiarucci A (2011) Geostatistical modelling of regional bird species richness: exploring environmental proxies for conservation purpose. Biodivers Conserv 20:1677–1694

Blondel J, Aronson J (1999) Biology and Wildlife of the Mediterranean region. Oxford University Press, Oxford

Chávez V, Macdonald SE (2005) The influence of canopy patch mosaics on understory plant community composition in boreal mixedwood forest. Forest Ecol Manag 259:1067–1075

Crawley MJ (1993) GLIM for ecologists. Blackwell Scientific Publications, Oxford

Criado C (1982) Nota geográfica sobre los sabinares de Anaga. VVAA Homenaje a Alfonso Trujillo. Aula de Cultura de Tenerife, Santa Cruz de Tenerife, pp 453–469

Cronk QCB, Fuller JL (1995) Plant invaders. The threat to natural ecosystems. Chapman and Hall, London

Currie DJ, Mittelbach GG, Cornell HW, Field R, Guégan JF, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff T, O'Brien EM, Turner JRG (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecol Lett 7:1121–1134

Del Arco M, Wildpret W, Pérez-de-Paz PL, Rodríguez-Delgado O, Acebes JR, García-Gallo A, Martín VE, Reyes-Betancort JA, Salas M, Bermejo JA, González R, Cabrera MV, García S (2006a) Mapa de vegetación de Canarias. GRAFCAN SL, Santa Cruz de Tenerife

Del Arco M, Pérez-de-Paz PL, Acebes JR, González-Mancebo JM, Reyes-Betancort JA, Bermejo JA, De Armas S, González-González R (2006b) Bioclimatology and climatophilous vegetation of Tenerife (Canary Islands). Ann Bot Fenn 43(3):167–192

Del Arco M, González-González R, Garzón-Machado V, Pizarro-Hernández B (2010) Actual and potential natural vegetation on the Canary Islands and its conservation status. Biodivers Conserv 19:3089–3140

Denslow JS, Space JC, Thomas PA (2009) Invasive exotic plants in the tropical pacific islands: patterns of diversity. Biotropica 41:162–170

Diodato N (2005) The influence of topographic co-variables on the spatial variability of precipitation over small regions of complex terrain. Int J Climatol 25:351–363

Dobson AJ (1990) An introduction to generalized linear models. Chapman and Hall, London

Dolan BJ, Parker JR (2005) Ecosystem classification in a flat, highly fragmented region of Indiana, USA. Forest Ecol Manag 219:109–131

Domínguez-Lozano F, Price J, Otto R, Fernández-Palacios JM (2010) Using taxonomic and phylogenetic evenness to compare diversification in two Island Floras. Perspect Plant Ecol Evol Syst 12:93–106

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–366

El-Bana M, Shaltout K, Khalafallah A, Mosallam H (2010) Ecological status of the Mediterranean *Juniperus phoenicea* L. Relicts in the desert mountains of North Sinai. Egypt Flora 205:71–178

Erre P, Chessa I, Nieddu G, Jones PG (2009) Diversity and spatial distribution of *Opuntia* spp. in the Mediterranean Basin. J Arid Environ 73:058–1066

Farjon A (2005) Monograph of Cupressaceae and Sciadopitys. Royal Botanic Gardens, Kew, London

Fernández-Palacios JM (1987) Análisis de la variación espacial de la vegetación de Tenerife e interpretación en términos ambientales. Doctoral thesis, Universidad de La Laguna (unpublished)

Fernández-Palacios JM (1992) Climatic response of plant species on Tenerife (Canary Island). J Veg Sci 3:595–602

Fernández-Palacios JM, de Nicolás JP (1995) Altitudinal pattern of vegetation variation on Tenerife. J Veg Sci 6:183–190

Fernández-Palacios JM, Otto R, Delgado JD, Arévalo JR, Naranjo A, González-Artiles F, Morici C, Barone R (2008) Los Bosques Termófilos de Canarias. Proyecto LIFE04/NAT/ES/000064. Excmo. Cabildo Insular de Tenerife, Santa Cruz de Tenerife

Gardner AS, Fisher M (1996) The distribution and status of the montane juniper woodlands of Oman. J Biogeogr 23:791–803

Gauch HG Jr (1982) Multivariate analysis in community ecology. Cambridge University Press, Cambridge

Gauquelin T, Bertaudiere V, Montes N, Badri W, Asmode JF (1999) Endangered stands of thuriferous juniper in the western Mediterranean basin: ecological status, conservation and Management. Biodivers Conserv 8:1479–1498

Gimeno I, Vilà M (2002) Recruitment of two *Opuntia* species invading abandoned olive groves. Acta Oecol 23:239–246

González-Artiles FJ (2006) El Bosque Termófilo de Gran Canaria. Doctoral thesis, Departamento de Biología, Universidad de Las Palmas de Gran Canaria

Hill MO, Gauch HG Jr (1980) Detrended correspondence analysis, an improved ordination technique. Vegetatio 42:47–58

Jakobs G, Kueffer C, Daehler CC (2010) Introduced weed richness across altitudinal gradients in Hawai'i: humps, humans and water-energy dynamics. Biol Invasions. doi:10.1007/s10530-010-9816-6

Körner C (2007) The use of "altitude" in ecological research. Trends Ecol Evol 22:569–574

Kreft H, Jetz W, Mutke J, Kier G, Barthlott W (2008) Global diversity of island floras from a macroecological perspective. Ecol Lett 11:116–127

Kueffer C, Daehler CC, Torres-Santana C, Lavergne C, Meyer JY, Otto R, Silva L (2010) A global comparison of invasive plant species on oceanic islands. Perspect Plant Ecol Evol Syst 12(2):145–161

Linares-Palomino R, Kvist LP, Aguirre-Mendoza Z, Gonzáles-Inca C (2010) Diversity and endemism of woody plant species in the Equatorial Pacific seasonally dry forests. Biodivers Conserv 19:169–185

Luis M, Fernández-Pello L, Quirantes F (2005) El papel de las transiciones laterales en el escalonamiento vegetal: el ejemplo del sabinar de Afur (Tenerife, Islas Canarias). In: VVAA Espacios públicos, espacios privados. Un debate sobre el territorio, pp 276–279

Mack RN, Simberloff D, Lonsdale WM, Evans HC, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences and control. Ecol Appl 10:689–710

Marrero MV, Rodríguez O, Wildpret W (1992) Contribución al estudio fitocorológico de los restos de sabinares y otras comunidades termófilas del Sur de Tenerife (Islas Canarias). Rev Acad Canar Cienc 3(4):25–44

Martín-Esquivel JL, García Court H, Redondo-Rojas CE, García-Fernández I, Carralero Jaime I (1995) La Red Canaria de Espacios Naturales Protegidos. Consejería de Política Territorial, Viceconsejería de Medio Ambiente, Gobierno de Canarias

Martín-Esquivel JL, Bethencourt J, Cuevas-Agulló E (2012) Assessment of global warming on the island of Tenerife, Canary Islands (Spain). Trends in minimum, maximum and mean temperatures since 1944. Clim Chang. doi:10.1007/s10584-012-0407-7

McCain CM (2007) Could temperature and water availability drive elevational species richness patterns? A global case study for bats. Global Ecol Biogeogr 16:1–13

McCullagh P, Nelder JA (1989) Generalized linear models. Chapman and Hall, London

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design. Gleneden Beach, El Oregón

McCune B, Mefford MJ (2011) PC-ORD. Multivariate analysis of ecological data. Version 6.0 MjM Software Design, Gleneden Beach, Oregon, USA

Médail F, Quézel P (1997) Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. Ann Mo Bot Gard 84:112–127

Milios E, Pipinis E, Petrou P, Akritidou S, Smiris P, Aslanidou M (2007) Structure and regeneration patterns of the *Juniperus excelsa* Bieb. stands in the central part of the Nestos valley in the northeast of Greece, in the context of anthropogenic disturbances and nurse plant facilitation. Ecol Res 22:713–723

Miller RF, Svejcar TJ, Rose JA (2000) Impacts of western juniper on plant community composition and structure. J Range Manag 53(6):574–585

Montesinos D, Otto R, Fernández Palacios JM (2009) 9560 Bosques endémicos de *Juniperus* spp. (*). In: VVAA Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España. Madrid: Ministerio de Medio Ambiente, y Medio Rural y Marino. Madrid, pp 84

Muñoz-Reinoso JC (2004) Diversity of maritime juniper woodlands. Forest Ecol Manag 192:267–276

Nezadal W, Welss W (2009) Aportaciones al conocimiento del bosque termófilo en el noroeste de Tenerife (Islas Canarias). In: Beltran-Tejera E, Afonso-Carillo J, García-Gallo A, Rodríguez-Delgado O (eds), Homenaje al profesor Dr. Wolfredo Wildpret de la Torre, Instituto de Estudios Canarios, La Laguna (Tenerife, Islas Canarias), Monografía, vol 78, pp 229–244

O'Brien EM, Field R, Whittaker RJ (2000) Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. Oikos 89:588–600

Otto R (2003) Spatial and temporal variability of succulent scrub on Tenerife and its ecological interpretation. Doctoral Thesis (English summary), Institute of Geography. University of Zürich

Otto R, Fernández-Palacios JM, Krüsi BO (2001) Variation in species composition and vegetation structure of succulent scrub on Tenerife in relation to environmental variation. J Veg Sci 12:237–248

Otto R, Krüsi BO, Delgado JD, Fernández-Palacios JM, García-del-Rey E, Arévalo JR (2010) Regeneration niche of the Canarian juniper: the role of adults, shrubs and environmental conditions. Ann For Sci. doi:10.1051/forest/2010034

Padrón B, Nogales M, Traveset A, Vilà M, Martínez-Abraín A, Padilla DP (2011) Integration of invasive *Opuntia* spp. by native and alien seed dispersers in the Mediterranean area and the Canary Islands. Biol Invasions 13:831–844

Pretto F, Celesti-Grapow L, Carli E, Blasi C (2010) Influence of past land use and current human disturbance on non-native plant species on small Italian islands. Plant Ecol 210:225–239

Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? Ecography 18:200–205

Reyes-Betancort JA, Wildpret W, del Arco M, Pérez-de-Paz PL (2001) The vegetation of Lanzarote (Canary Islands). Phytocoenologia 31:185–247

Rivas-Martínez S, Wildpret M, del Arco M, Rodríguez O, Pérez-de-Paz PL, García-Gallo A, Acebes JR, Díaz-González TE, Fernández-González F (1993) Las comunidades vegetales de la Isla de Tenerife (Islas Canarias). Itinera Geobot 7:169–374

Rodríguez O, Marrero MV (1991) Evolución y aprovechamiento de los bosques termófilos (los "montes bajos") de la Isla de Tenerife. Anuario de Estudios Atlánticos 36, pp 595–630

Rodríguez O, Wildpret W, del Arco M, Pérez-de-Paz PL (1990) Contribución al estudio fitosociológico de los restos de sabinares y otras comunidades termófilas de la Isla de Tenerfie (Canarias). Rev Acad Canar Cienc 2:121–142

Rosenzweig ML, Abramsky Z (1993) How are Diversity and Productivity related? In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities. University of Chicago Press, Chicago, pp 52–65

Santos A, Fernández M (1983) Vegetación del macizo de Teno. Datos para su conservación. Comunic II Congr Pro-Flora Macaronésica 1977:385–424

Scott JM, Murray M, Wright RG, Csuti B, Morgan P, Pressey RL (2001) Representation of natural vegetation in protected areas: capturing the geographic range. Biodivers Conserv 10:1297–1301

Steinbauer MJ, Otto R, Naranjo-Cigala A, Beierkuhnlein C, Fernández-Palacios JM (2011) Increase of island endemism with altitude-speciation processes on oceanic islands. Ecography. doi: 10.1111/j.1600-0587.2011.07064.x

Stierstorfer C, von Gaisberg M (2006) Annotated checklist and distribution of the vascular plants of El Hierro, Canary Islands, Spain. Englera 27:1–221

Sventenius ERS (1946) Notas sobre la flora de las Cañadas de Tenerife. Boletín Instituto Nacional de Investigaciones Agronómicas 15(78):149–171

Ter Braak CJF, Smilauer P (1998) CANOCO reference manual and user's guide to Canoco for windows, software for canonical community ordination (version 4). Microcomputer Power, Ithaca

Terrab A, Schönswetter P, Talavera S, Vela E, Stuessy TF (2008) Range-wide phylogeography of *Juniperus thurifera* L., a presumptive keystone species of western Mediterranean. Mol Phylogenet Evol 48(1):94–102

Thompson JD (1999) Population differentiation in Mediterranean plants: insights into colonization history and the evolution and conservation of endemic species. Heredity 82:229–236

Vilà M, Burriel JA, Pino J, Chamizo J, Llach E, Porterias M, Vives M (2003) Association between *Opuntia* species invasion and changes in land-cover in the Mediterranean region. Glob Chang Biol 9:1234–1239

von Gaisberg M (2005) Die Vegetation der Fußstufe von El Hierro (Kanarische Inseln). Diss Bot 395:1–364

Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography. Ecology, evolution and conservation. Oxford University Press, New York

Zobel M, Otto R, Laanisto L, Naranjo-Cigala A, Pärtel M, Fernández-Palacios JM (2011) The formation of species pools: historical habitat abundance affects current local diversity. Global Ecol Biogeogr 20(2):251–259

Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data. Springer, USA