

Modelling invasive plant alien species richness in Tenerife (Canary Islands) using Bayesian Generalised Linear Spatial Models

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Abstract Biological invasions are one of the major threats to biodiversity, especially on islands where the number of endemic species is the highest despite their small area. In the Canary Islands, the relationships among invasive alien species (hereafter IAS) and their environmental and anthropogenic determinants have been thoroughly described but robust provisional models integrating species spatial autocorrelation and patterns of IAS communities are still lacking. In this study, we developed a Generalised Linear Spatial Model for Invasive Alien Species Richness (IASR) under a Bayesian framework, using a methodological approach that encompasses GIS and geostatistical analysis. In this study, we hypothesised that the inclusion of spatial autocorrelation can improve model performance thus obtaining more IASR-reliable predictions. In addition, this method provides uncertainty maps that prioritize areas where further sampling efforts are needed. Our model showed that IASR in Tenerife is mainly driven by a combination of anthropogenic and natural processes, highlighting favourable conditions for IAS from the coastline to about 800 m a.s.l., especially on the windward humid aspect. Among anthropogenic factors, a clear positive relationship between road kernel density estimation and IASR was found. Indeed, road density has recently increased especially in low to mid altitudinal zones on the Canary Islands, strictly associated with urban expansion and it has been widely demonstrated to be one of the main IAS pathways. Hence, higher road density can be related to increased 'propagule pressure' which is, together with source of disturbance, one of the most important factors explaining richness in alien species invasion success. Our main conclusions highlight the importance of considering spatial autocorrelation and researchers' prior knowledge to increase the predictive power of statistical models. From a practical perspective, these models and their related uncertainty, will serve as important management tools highlighting those portions of territories that will be more prone to biological invasions and where monitoring efforts should be directed.

Keywords: biodiversity, biogeography, biological invasions, geostatistics, GIS, kriging

INTRODUCTION

Islands display unique ecological and evolutionary processes, hosting more than 20% of the terrestrial plant and vertebrate species in the world, within less than 5% of the global terrestrial area (Courchamp, et al., 2014). Endemics on islands are present with a magnitude higher than on continents (Kier, et al., 2009). In fact, more than one third of biodiversity hotspots in the world are entirely, or largely, within islands (Bellard, et al., 2014).

Besides their high diversity, islands host extremely fragile environments: 50 out of 80 of the documented plant extinctions in the last 400 years occurred on islands and more than 2000 endemic island taxa are currently thought to be on the verge of extinction (Ricketts, et al., 2005; Whittaker & Fernández-Palacios, 2007; Fernández-Palacios, et al., 2015). Nowhere in Europe is this pattern more conspicuous than in Macaronesia, the biogeographic region that encompasses the oceanic islands of the Azores, Madeira, the Canaries and the Cape Verde archipelago (Whittaker & Fernández-Palacios, 2007; Fernández-Palacios, et al., 2015). Macaronesia is widely recognised as an outstanding biodiversity hotspot worldwide due to its high rates of endemism in angiosperms and in bryophytes (40% and 6.5%, respectively, Whittaker & Fernández-Palacios, 2007).

Invasive Alien Species (IAS) pose a serious threat to the conservation of biodiversity and ecosystem integrity worldwide (DAISIE, 2009; Scalera, et al., 2012). Island systems, in fact, are extremely susceptible to biological invasions due to low habitat diversity, their simplified trophic webs and higher rate of endemic

species (Courchamp, et al., 2003; Millennium Ecosystem Assessment, 2005; Vilà & Lopez-Darias, 2006; Barni, et al., 2012; Bacaro, et al., 2015).

Oceanic islands perform as an *open-air laboratory* in the field of invasion biology, because of their long history of large-scale anthropogenic disturbances and the recent introduction of non-native species (Whittaker & Fernández-Palacios, 2007; Denslow, et al., 2009), allowing us to generalise about the outcome of biotic invasions and to test the consistency of invasive organisms' behaviours (Kueffer, et al., 2010).

Several factors may determine the composition and the abundance of alien floras, including climate, geology, land use, landscape context, human impact, competition with natives and natural or anthropogenic disturbance and residence time (Crawley, 1987; Pyšek, et al., 2002; Arévalo, et al., 2005). Anthropogenic factors, such as inhabitants and trade networks, were imputed as main drivers of plant IAS introduction and spread: most populated islands should have more opportunities to import (and export) novel species due to the high rate of trade and transport with mainland areas (Pyšek, et al., 2010). Roads are anthropogenic features that can have greater influence on the distribution of IAS, particularly increasing the IAS propagule pressure (Lockwood, et al., 2005) or promoting the spread of generalist species with short life cycles and high reproductive rates (Parendes & Jones, 2000; Pauchard & Alaback, 2004; Arévalo, et al., 2005; Dietz & Edwards, 2006; Arteaga, et al., 2009). In the Canary archipelago, as well as worldwide (Pauchard, et

al., 2009), elevation and topography are factors driving the structure and distribution patterns of alien species spread (Arévalo, et al., 2005; Rejmánek, et al., 2005; Arteaga, et al., 2009)

Ecologists agree on the need for preventive tools such as early alert systems, given that control or eradication of already-established populations is more difficult and costly (Hobbs & Humphries, 1995; Bax, et al., 2001). Predictive invasion models, in fact, allow for evaluating the present and future extent of plant invasions. Furthermore, their outcomes are useful tools supporting the development of eradication/control programmes (Wace, 1977; Alpert, et al., 2000; Rejmánek & Pitcairn, 2002).

Spatial autocorrelation (SAC) is rarely included in ecological models thus potentially leading to biased parameter estimates. Furthermore, classic geostatistical models assume that data are Gaussian distributed, which may be an unrealistic assumption for count data, such as species richness. Generalised linear spatial models (GLSMs) provide a more robust model definition able to cope with response variables belonging to the exponential family distribution (Diggle, et al., 1998, 2003; Zhang, 2002; Christensen & Waagepetersen, 2002; Diggle & Ribeiro, 2007). By definition, the GLSM is a generalised linear mixed model in which the random effects are derived from a spatial process. The Bayesian approach allows parameter estimation by combining information coming from the observed data (via the likelihood function) as well as information coming from other prior sources (i.e. previous studies, subjective judgments) which is formalised through prior distributions. Therefore, Bayesian GLSMs (BGLSM) offer a flexible and robust approach for incorporating spatial correlation and prior knowledge into the modelling approach. In addition, the possibility of obtaining uncertainty maps may provide useful information where data are missing and further sampling efforts should be addressed. In this study, we hypothesised that the inclusion of SAC can improve model performance and therefore more reliable predictions, assuming that a variable selection process has been adopted. Specifically, we investigated alien species richness distribution on Tenerife (Canary Islands) using a multidisciplinary approach encompassing Geographic Information Systems (GIS), geostatistical calculation and statistical modelling. The main goals of this study are: i) to compute an ecologically and spatially reliable model of ASR spatial pattern in the island ii) to test if the inclusion of SAC into the modelling framework improves model performance.

MATERIALS AND METHODS

Study area

The study was carried out on Tenerife, the largest (2,033 km²) island of the volcanic Canary archipelago situated in the subtropics ca. 70 km off the northwest coast of Africa (27–29° N, 13–18° W; Fig. 1). It is characterised by steep altitudinal gradient and it has a triangle-based pyramid shape with a truncated apex at 2,000 m a.s.l. at Las Cañadas, from which the volcano Teide rises (3,718 m a.s.l.)

The climate on Tenerife is semiarid to humid Mediterranean type (Arteaga, et al., 2009), with mean annual temperature reaching 19° C on the windward aspect and 21° C on the leeward one. Mesoclimate is affected by trade winds that create a contrast between the northern and windward aspect (more humid and cloudy) and the southern and leeward aspect (more arid and cloudless).

Strong variation in elevation 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 & Fernández-Palacios, 2007). On Tenerife, vegetation can be simplified into five ecosystems based mainly on elevation and orientation gradients: succulent coastal scrub (0–700 m a.s.l.), thermophilous forest (200–600 m), laurel forest or *laurisilva* (500–1,000 m), Canarian pine forest (800–2,000 m), and summit or high-mountain scrub (> 2,000 m) (Fernández-Palacios, 1992; del Arco Aguilar, et al. 2006).

Statistical methods

Response variable

The distribution of Invasive Alien Species on the Canary Islands is available at ATLANTIS (Gobierno de Canarias, 2016). This database contains the occurrences of alien species within a grid of 500 m × 500 m square cells covering the entire archipelago. Species records span from 1970 to 2013. Invasive Alien Species Richness (IASR) on Tenerife was obtained by aggregating species occurrences in those ATLANTIS grid cells covering Tenerife Island land (5,514 cells out of 8,519 selected). Seventy-two species are present in the dataset (out of 701 alien species reported for the entire archipelago; Archavaleta, et al., 2010).

Predictor variables

Three sets of abiotic variables, namely landscape, anthropogenic and climatic predictors, were derived in order to take into account all the the potential factors

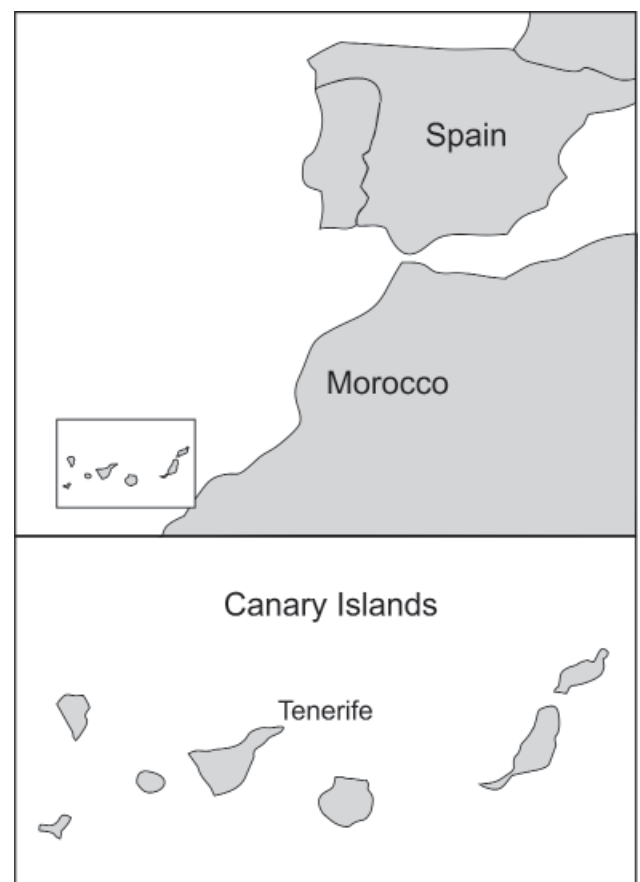


Fig. 1 Canary Islands and position of Tenerife Island within the Canary archipelago.

influencing alien species richness. Specifications of the variables chosen are addressed below.

Landscape predictors

The Digital Elevation Model (DEM) was downloaded from Cartográfica de Canarias S.A. (GRAFCAN, <<https://www.grafcan.es/>>). Aspect and slope were derived from the DEM for each 10 × 10 m pixel using QGIS 2.16.0 with GRASS 7.0.4 (Quantum GIS Development Team, 2016). The standard deviation of slope was calculated as an index of roughness (Grohmann, et al., 2010).

All the predictors were resampled to 500 m of spatial resolution using the nearest neighbour algorithm, accordingly to the spatial resolution of the species abundance grid. The relative abundance of vegetation classes (del Arco Aguilar, et al., 2010) within each cell was used to classify each grid cell, while the percentage of protected area per cell was used as a proxy of landscape nature conservation.

Anthropogenic predictors

As a proxy of anthropogenic impacts (e.g. fragmentation, Bacaro, et al., 2011) the Shannon index based on the relative abundance of land use classes within each cell was computed using the R package “*vegan*” (Oksanen, et al., 2017). We calculated a density proxy for roads using a Kernel density estimation (Rosenblatt, 1956; Parzen, 1962) using four regularly distributed classes of sample points on the road network distant from each other 5, 10, 20 and 50 km. As above, data were downloaded from Cartográfica de Canarias S.A.

Climate predictors

Climatic data were obtained from Agencia Estatal de Meteorología (AEMET) spanning from 2005 to 2014. Since recorded data showed many gaps throughout the entire time series of every single weather station, we used only those weather stations having records covering at least 80% of the full-time series for Precipitation (P) and 60% for Temperatures (T).

For each dataset mean annual (ma), mean seasonal (Winter: December, January, February (DJF); Spring: March, April, May (MAM); Summer: June, July, August (JJA)) were calculated. In order to obtain continuous representation of the phenomena, the co-kriging spatial interpolation technique (Myers, 1984) was applied using elevation, slope and aspect as covariates using “*geoR*” R package (Ribeiro & Diggle, 2001).

Data analysis and modelling

Spatial autocorrelation in explanatory variables was checked by computing Moran’s I, using R package “*spdep*” (Bivand & Piras, 2015). In order to avoid multicollinearity, a forward variable selection with a double-stopping criterion approach (Blanchet, et al., 2008) was adopted in order to select the reduced set of predictors using “*adespatial*” (Dray, et al., 2017).

This procedure consists of computing the global model explained by all explanatory variables via a constrained ordination such as Redundancy Analysis and, if the resulting model is significant, calculating the adjusted coefficient of multiple determination (R^2_{adj}). Then variables were added to a null model (including only the intercept) using a forward procedure: the procedure stops when no more significant variables were founded (for a given alpha level) or when the R^2_{adj} of the model is greater than the global model R^2_{adj} . This double-stopping criterion should prevent the selection method from being too liberal and consequently inflating type I error rates. Once the reduced set of predictors was obtained, this was further evaluated via AIC comparisons using an iterative automatic routine (package “*glmulti*”, Calcagno & de Mazancourt, 2010). The set of predictors thus obtained was then used for computing the BGLSM. The resulting model was used as a starting point for the BGLSM.

Unfortunately, probably as an effect of the high number of predictors retained in model selection, we came across issues in algorithm convergence. For this reason, we decided to further reduce the number of predictors chosen, among the reduced list previously obtained, to three which are known to be important drivers of the alien species community along the elevation gradient (Arévalo, et al., 2005, 2010; Barni, et al., 2012; Bacaro, et al., 2015). Thus, only the roads 10 km kernel density, P_{MAM} and elevation were included in the final model (Table 1).

To take into account the spatial correlation of count data, a BGLSM using the Langevin-Hastings Markov Chain Monte Carlo (MCMC) algorithm was computed using the “*geoRglm*” R package (Christensen & Ribeiro, 2002). To complete the Bayesian model formulation of the geostatistical models, a strong-informative uniform prior distribution (Rocchini, et al., 2017a) based on the result of the geostatistical model was specified. Simulations were run with the following specifications: four chains, 20,000 iterations, burn-in period of 6,000 iterations and a thinning rate of 100. To ensure a good mixing of the chains, convergences were assessed both visually and with Geweke’s diagnostic (Geweke, 1992), along with the autocorrelation within the chains through “*coda*” package (Plummer, et al., 2006). The Bayesian framework also allows uncertainty of the model to be taken into account, that is the uncertainty of the prediction in the sampling units (Gelman & Hill, 2006). This statistic is crucial for correctly interpreting results and avoiding inappropriate decision-making.

Finally, the linear relationship between Predicted vs Observed IASR values was evaluated and the R^2 was calculated as a measure of goodness of fit.

All analyses were performed using the R 3.4 environment (R Core Team, 2017).

RESULTS

A total of 72 IAS were present in the dataset, with a mean of 4.18 species per cell (range: 1–27). The most common species on the island are *Opuntia maxima* (3,161

Table 1 Summary statistics of predictors used in the MAM. The variables units are shown in the last column.

	Mean	1st quantile	3rd quantile	Min	Max	Units
Roads 10 km kernel density	0.06523	0.02160	0.08953	0.00010	0.41928	-
$P_{MAM2005-2014}$	25.808	14.878	36.546	1.647	63.103	mm
Elevation	578.9934	240.0000	794.0460	0.5685	2421.3621	m

occurrences), *Ageratina adenophora* (2,239 occurrences) and *Ricinus communis* (1,615 occurrences). On average, the northern (and windward) part of the island has higher values than the southern (Fig. 2), where the biggest cities are (Santa Cruz de Tenerife and San Cristóbal de La Laguna

on the NNE coast, Puerto de La Cruz on the NW coast). Furthermore, a decreasing altitudinal trend in IASR was also observed, with higher values of IASR near the coast and lower values above 1,500 m a.s.l. SAC in IASR values were confirmed by the Moran's Index value ($I = 0.873, p < 0.001$).

Table 2 Model output derived from the maximum likelihood analysis: τ^2 is the nugget, σ^2 is the sill, Φ is the range and gives information about the spatial autocorrelation of the sampling units.

Variables	Coefficients
Intercept	3.4966
Roads 10 km kernel density	18.7518
$P_{MAM2005-2014}$	0.0126
Elevation	-0.0017
τ^2	5.7100
σ^2	10.7700
Φ	2.8950

The inclusion of SAC in the minimum adequate model resulted in a consistent improvement in general model performance (ΔAIC 7,366). In the BGLMS, Markov chains show good mixing and convergence as highlighted by Geweke's diagnostics. Positive linear relationships of IASR were observed with road kernel density estimation (10 km) and $P_{MAM2005-2014}$, while elevation showed a negative trend (Table 2). Suitable areas for IAS appear to be located in urban areas, especially on the humid leeward aspect of the island (Fig. 3). Model output summarised in Table 3 and Fig. 4 shows the uncertainty in the predicted IASR

Table 3 Descriptive statistics of model outputs.

	Mean	1st quantile	3rd quantile	Min	Max
Predicted	3.47	1.29	4.44	0.33	27.39
Uncertainty	0.75	0.40	0.90	0.14	4.48

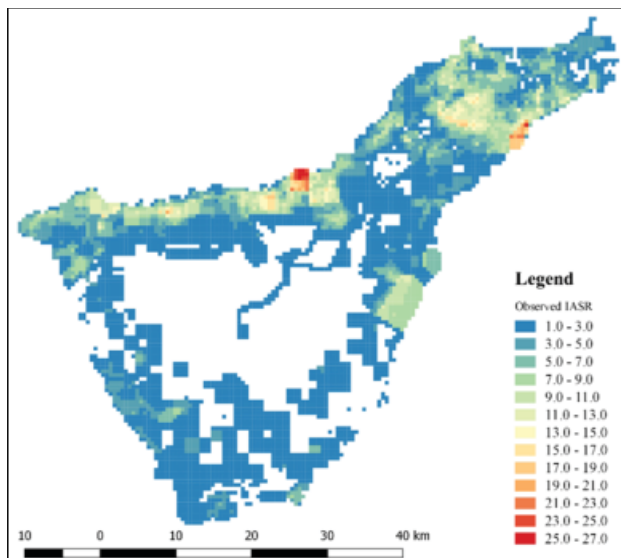


Fig. 2 Spatial pattern of alien species richness in Tenerife island.

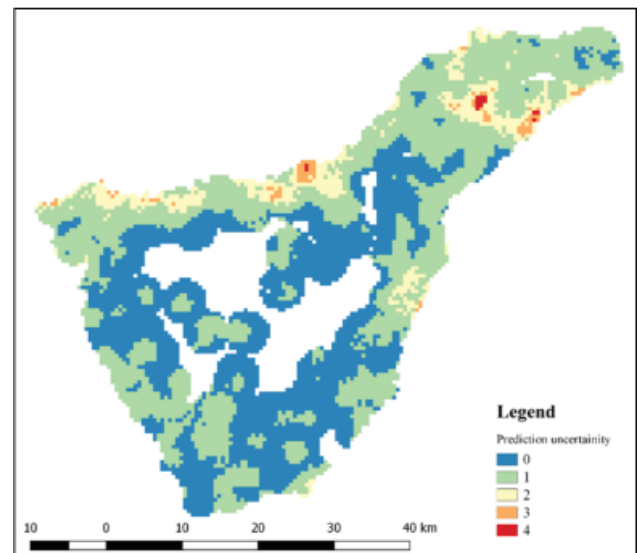


Fig. 4 Spatial pattern of uncertainty of the prediction of invasive alien species richness by BGLSM.

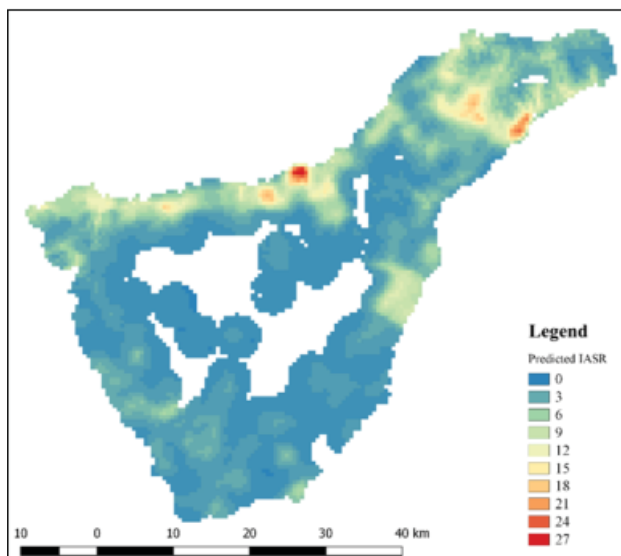


Fig. 3 Spatial pattern of predicted invasive alien species richness by BGLSM.

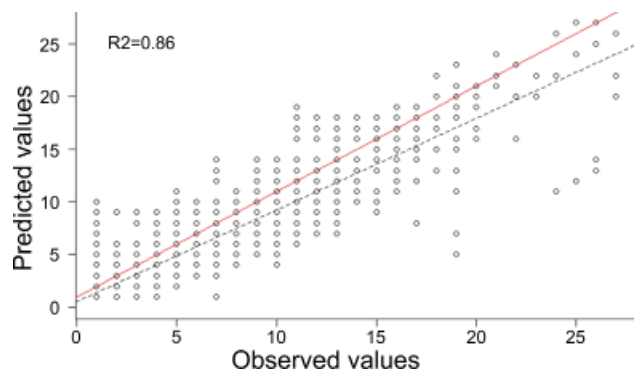


Fig. 5 Predicted vs. observed alien species richness. The solid line represents best prediction line, dashed line the fitted linear model.

values. Figure 5 shows the predicted *versus* observed values scatterplot suggesting a good performance of model fit.

DISCUSSION

The approach used in the selection of covariates and the incorporation of the spatial autocorrelation leads us to build a reliable ecological model to understand the IASR behaviour on Tenerife Island (Fig. 5). The outcomes of the model largely agree with most of the results previously published in the literature, taking into consideration both natural and anthropogenic processes. However, the Δ AIC suggests that incorporating SAC into GLM allows a consistent improvement in general model performance. Moreover, it allows us to obtain maps of the predictions that can be easily consulted by local governments. The map of uncertainty of the prediction provided in the Bayesian framework represents a powerful tool to highlight those areas where sampling efforts should be directed, providing valuable guidance in the decision-making process. On average, uncertainty in the model was quite low and evenly dispersed across the island. The areas where the uncertainty was higher are where human-related land uses occur, mainly in the arid coastal belt at low elevations (Fernández-Palacios & Nicolás, 1995; Rocchini, et al., 2017b).

The Canary Islands, particularly Tenerife Island, are chiefly characterised by a steep altitudinal gradient causing potential variations in several abiotic conditions such as water availability, temperature, precipitation, and solar radiation even over relatively short distances (Alexander, et al. 2009). IASR is inversely proportional with elevation as already observed in Arévalo, et al. (2005), Arteaga, et al. (2009) and Bacaro, et al. (2015), among others. The positive relationship between elevation and limiting factors such as drought, low temperatures and solar radiation were thoroughly investigated. Accordingly, it has been observed that at higher elevations, thermic and hydric stresses reduce the number of successful colonisations of alien species in different regions of the world (Fernandez-Palacios, 1992; Alpert, et al., 2000; Godfree, et al., 2004; Pauchard & Alaback, 2004; Becker, et al., 2005).

In general, mild environmental conditions associated with reduced drought stress enhance alien establishment and spread (Whittaker & Heegaard, 2003). These conditions were found at ca. 800–1,000 m a.s.l. (Arévalo, et al., 2005; Arteaga, et al., 2009). It has been observed that invasion success is mainly linked to the biogeographical affinities and environmental tolerances of the species (Wilson, et al., 1992; Arévalo, et al., 2005; Daehler, 2005). Accordingly, we found a positive relationship between P_{MAM} and IASR, and the BGLSM highlights as suitable the humid areas below 1000 m a.s.l, especially on the windward aspect, whereas the model did not predict suitable areas above 1500 m, except where roads are present. These findings reflect well the same pattern already observed in other studies performed both in Tenerife and in other oceanic islands (e.g. Arévalo, et al., 2005, Pauchard, et al., 2009; Bacaro, et al., 2015). In addition, Daehler (2005) observed similar patterns on the islands of Hawaii, where the relative importance of temperate species on the community composition increased strongly above 1,400 m a.s.l to detriment of the tropical ones.

Other authors (e.g. Nogués-Bravo, et al., 2008; Marini, et al., 2013) pointed out that relationships between IASR and anthropogenic factors are concentrated at low elevations, consequently increasing the opportunities

for the introduction and establishment of propagules. Accordingly, our results showed a peak of alien species richness at a relatively low elevation. Species might have been introduced in the lowlands from different sources and in several historical periods. The kernel road density estimation shows a clear positive relationship with IASR. Bacaro, et al. (2015) reported that alien species were absent from plots located at higher elevation in plots sampled near the main Tenerife road network, consistent with previous observations (Pauchard & Alaback, 2004). Road density has increased especially in low to mid elevation belts of the Canary Islands, strictly associated with urban expansion and, consequently, to the spread of exotic plants. Roads may facilitate the dispersal of propagules of alien species via three main mechanisms: 1) as a source of disturbance that creates new environmental conditions that are suitable to ruderal and pioneer species; 2) they may facilitate the dispersal of propagules via air movement associated with the transit of vehicles; and 3) they may boost the rate of invasion by reducing competitiveness of native species that can cause the potential disappearance of even entire stands (Trombulak & Frissel, 2000; Bacaro, et al., 2015).

In this study, we assessed the incorporation of SAC into an ecological model built using ecologically reliable predictors. The incorporation of SAC improved general model performance and allows for uncertainty to be accounted for in the model framework, providing a way to prioritize areas where more survey is needed along with further monitoring actions in order to reduce uncertainty.

Mild environmental conditions may be responsible for quick establishment and dispersal of aliens on islands. Accordingly, compared with current literature, our results showed higher alien species richness in mild environmental conditions and at a relatively low elevation. This can be also due to the fact that human land use is concentrated at low elevations, consequently increasing the opportunities for the introduction and establishment of propagules. To cope with plant alien species invasion, local governments have tried different approaches (Foxcroft, et al., 2007) but the most effective method still remains mechanical or hand removal (Gobierno de Canarias, 2014). In a global warming scenario, a modelling approach that takes into account spatial autocorrelation of data may play an even more crucial role in alien species monitoring, highlighting those portions of territories that are more prone to biological invasions, especially in fragile ecosystems such as in the Canary Islands.

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