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Original Research Article

A spatially-explicit model of alien plant richness in Tenerife (Canary Islands)

Daniele Da Re[a,*], Enrico Tordoni[a], Zaira Negrín Pérez[b], José María Fernández-Palacios[b], José Rámon Arévalo[b], Rüdiger Otto[b], Duccio Rocchini[c,d,e], Giovanni Bacaro[a]

[a] Department of Life Sciences, University of Trieste, Via L. Giorgieri 10, 34127 Trieste, Italy
[b] Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de La Laguna, Avenida Astrofísico Francisco Sánchez s/n, 38205 La Laguna, Tenerife, Spain
[c] Center Agriculture Food Environment (C3A), University of Trento, Via E. Mach 1, 38010 S. Michele all'Adige, Trentino, Italy
[d] Department of Cellular, Computational and Integrative Biology - CIBIO, University of Trento, Via Sommarive 14, 38123 Povo, Trentino, Italy
[e] Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, Via E. Mach 1, 38010 S. Michele all'Adige, Trentino, Italy

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ABSTRACT

Biological invasions are one of the major threats to biodiversity, especially in oceanic islands. In the Canary Islands, the relationships between plant Alien Species Richness (ASR) and their environmental and anthropogenic determinants were thoroughly investigated using ecological models. However, previous predictive models rarely accounted for spatial autocorrelation (SAC) and uncertainty of predictions, thus missing crucial information related to model accuracy and predictions reliability. In this study, we propose a Generalized Linear Spatial Model (GLSM) for ASR under a Bayesian framework on Tenerife Island. Our aim is to test whether the inclusion of SAC into the modelling framework could improve model performance resulting in more reliable predictions. Results demonstrated as accounting for SAC dramatically reduced the model's AIC (ΔAIC = 4423) and error magnitudes, showing also better performances in terms of goodness of fit. Calculation of uncertainty related to predicted values pointed out those areas where either the number of observations (e.g. under-sampled areas) or the reliability of the environmental predictors was lower (e.g. low spatial resolution in highly heterogeneous environments). Although our results confirmed what was already observed in other ecological studies, such as the important role of roads in ASR spread, methodological considerations on the applied modelling approach point out the importance of considering spatial autocorrelation and researcher's prior knowledge to increase the predictive power of statistical models as well as the correctness in terms of coefficients estimates. The proposed approach may serve as an essential management tools highlighting those portions of territory that will be more prone to biological invasions and where monitoring efforts should be addressed.

1. Introduction

Conservation biologists are in urgent need for management tools to prevent biological invasions, since control or eradication of already-established populations is more difficult and costly (Bax et al., 2001; Rejmánek and Pitcairn, 2002; Hoffmann and Broadhurst, 2016). Ecological models are widely used to evaluate patterns and extent of alien species invasion, allowing the investigation of their driving factors (e.g. Kleinbauer et al., 2010; Bezeng et al., 2015, 2017; Dyderski et al., 2018).

In these models, however, spatial autocorrelation (SAC) may strongly affect models' outcomes, such as the estimates of the coefficients values and sign (Kühn, 2007). Nonetheless, SAC was rarely included in the ecological modelling process (Dormann et al., 2007). In practical term, SAC manifests when spatially closed observations present values more related than those further away from each other (i.e. lack of spatial independence of observation). Another methodological consideration on previously discussed modelling approaches is that classic linear models assume Gaussian-distributed residuals, which may be unrealistic when the response variable is a count data, such as in the case of species richness. Conversely, generalized linear spatial models (GLSMs; Diggle et al., 1998, 2003; Zhang, 2002; Christensen and Waagepetersen, 2002; Diggle and Ribeiro, 2007) provide an extension of the generalized linear model definition (McCullagh and

Abbreviations: ASR, Alien Species Richness; GIS, Geographic Information Systems; GLM, Generalized Linear Models; GLSM, Generalized Linear Spatial Model; BGLSM, Bayesian Generalized Linear Spatial Model; MCMC, Markov Chain Monte Carlo; MEA, Mean Absolute Error; RMSE, Root Mean Square Error; SAC, Spatial autocorrelation

* Corresponding author at: Earth and Life Institute, Université catholique de Louvain (UCLouvain), Place Louis Pasteur 3-L4.03.0, 1348 Louvain-la-Neuve, Belgium.
E-mail address: daniele.dare@uclouvain.be (D. Da Re).

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Nelder, 1989) since they are able to cope with response variables belonging to the exponential family distribution (Poisson, Gamma, Binomial) and allow to explicitly incorporate SAC into the modelling framework. By means of GLSMs, ecologists and invasion biologists can take advantage of the kriging methodology within the framework of the generalized linear model, thus providing spatially-explicit predictions of the investigated variable (Diggle et al., 1998; Lyashevska et al., 2016). Furthermore, spatial models provide uncertainty maps of those areas where the reliability of the environmental predictors is lower (e.g. low spatial resolution in highly heterogeneous environments) or where further sampling efforts are required (Bacaro et al., 2011; Rocchini et al., 2011). Recently, Bayesian GLSMs (hereafter BGLSM, Diggle and Ribeiro, 2007; Recta et al., 2012; Boyd et al., 2014) were proposed, which offer a flexible and robust approach for incorporating spatial autocorrelation and prior knowledge into the modelling framework (Rocchini et al., 2017).

To test for GLSM applications in a real context, and to compare their performances with previous developed non-spatial models, a data set on invasive alien species collected in Tenerife Island (Canary Archipelago) was selected as case study. On Oceanic islands, ecological and evolutionary processes produced unique assemblages of species, extremely rich in endemics (Whittaker and Fernández-Palacios, 2007). Accordingly, due to their complex habitat diversity and the high rate of endemism, island systems are extremely vulnerable to biodiversity loss because of numerous co-occurring pressures (e.g. sea-level rise, urban sprawl and habitat fragmentation) (Courchamp et al., 2003, 2014; Sax and Gaines, 2008; Bacaro et al., 2015). Among these, biological invasions represent one of the major threats to island biodiversity and ecosystem integrity (DAISIE, 2009; Scalera et al., 2012) decreasing local plant species diversity and impacting on nutrient cycling and ecosystem services (e.g. Vilà et al., 2011; Russell et al., 2017).

In the Canary archipelago, several studies explored the main drivers of plant alien species richness (Arévalo et al., 2005, 2008; Arteaga et al., 2009; Alexander et al., 2011; Bacaro et al., 2015). In these studies, elevation and topography are constantly invoked as those factors driving the structure and the distribution patterns of both alien and native plants in those islands (Arévalo et al., 2005; Arteaga et al., 2009) as well as worldwide (Rejmánek et al., 2005; Pauchard et al., 2009). Nonetheless, none of them explicitly address for SAC in the applied modelling approach. In this study, the distribution of plant alien species richness (hereafter ASR) on Tenerife was modelled using a multidisciplinary approach, which encompasses GIS, geostatistical calculation and Bayesian statistics. Our main goal is to assess if and how SAC inclusion within the modelling framework is responsible for the improvement of model performances and predictions, producing more ecologically reliable results in terms of higher predictive accuracy.

2. Materials and methods

2.1. Study area

The study was carried out on Tenerife, the largest island (2033 km^2) of the volcanic Canary archipelago (27–29° latitude N, 13–18° longitude W; Fig. 1). Located in the subtropics ca. 100 km off the NW-coast of Africa, Tenerife had a triangle-based pyramid shape with a truncated apex at 2000 m a.s.l. at Las Cañadas, from which the volcano Teide raised with a peak reaching 3718 m a.s.l., the highest in Macaronesia. Tenerife is also the most populated island of Macaronesia with approx. 0.9 million inhabitants and a population density of 438 people/km^2 (Instituto Nacional de Estadística, 2016).

The climate on Tenerife is semiarid to humid Mediterranean type (Huetz de Lemps, 1969; Arteaga et al., 2009), with mean annual temperature reaching 19 °C at the windward coast, 21 °C at the leeward coast and about 3 °C on the summit. Due to the subtropical climate, slight annual and daily fluctuations of temperature occurred. On the leeward slopes, mean annual temperature decreases with altitude from 21 °C at sea level to 14.3 °C at 1500 m a.s.l. reaching the lowest value of 9.8 °C at 2300 m a.s.l (Teide National Park). Mean annual precipitation is different according to the habitat considered, ranging from 130 mm on the coastline to 1000 mm in laurel forest areas (600–1200 m a.s.l.; Fernández-Palacios, 1992; Díaz-Díaz et al., 1999). Mesoclimate is affected by the trade winds that created an abrupt contrast between the northern or windward aspect (more humid and cloudy) and the southern or leeward aspect (more arid and cloudless).

3. Statistical methods

3.1. Response variable

Richness of plant alien species within a grid of 500 × 500 m square cells covering the entire Canary archipelago was downloaded from ATLANTIS database (Gobierno de Canarias, 2016; http//:www.biodiversidadcanarias.es). Species records spanned from 1970 to 2013. Out of the total 8519 cells available covering the whole Canary archipelago, only 5515 covering Tenerife island landmass were selected. The total number of different alien species was 72 for the set of cells, out of the 701 described by Arechavaleta et al. (2010) for the whole Canary archipelago.

3.2. Abiotic variables

Six explanatory variables (elevation, October-March precipitation, precipitation seasonality, spring mean minimum temperature, spring minimum temperature seasonality and road density) were selected as predictors of ASR on Tenerife Island. The rationale behind predictors' selection is that these six represent those factors included in previous models developed in Tenerife to describe plant alien richness: this selection was thought in order to provide a comparable set of variables to test for models differences in terms of explicative power including and excluding SAC, without the differences due to the predictors themselves.

In previous studies, Arévalo et al. (2005) and Bacaro et al. (2015) found elevation as the main factor shaping ASR in the study area. Arévalo et al. (2005) showed that mesic areas as more subjected to plant invasion, along with anthropogenic factors such as road density (Bacaro et al., 2015). Human activities represented one of the main factors enhancing alien species spread, facilitating species dispersion and providing new sources of introduction (Pyšek et al., 2010). Road density can be deemed as a good surrogate of propagule pressure and alien dispersion, because roads are a primary pathway of introduction and roadsides may serve as invasion epicenter, especially for annual species having high reproductive rates (Pauchard and Alaback, 2004; Bacaro et al., 2015). Finally, precipitation is known to influence growth and distribution of vascular plants and in Canary Islands 87.3% of the annual precipitation occurred in October-March (Sánchez-Benítez et al., 2017). Moreover, ASR distribution along elevation gradient is negatively affected by spring minimum temperature (Barni et al., 2012).

A Digital Elevation Model (DEM, 10 m of spatial resolution) and road network of Tenerife Island were downloaded from *Cartográfica de Canarias S.A.* (GRAFCAN, https://www.grafcan.es/, accessed on March 2016). Monthly precipitation of October-March periods and monthly temperature of March-May periods, spanning from 2005 to 2014, were obtained from Agencia Estatal de Meteorología (AEMET, accessed 13/04/2016). We used the climatic data collected by meteorological stations covering at least 60% of the full-time series within these periods, due to the presence of gaps occurring in the precipitation and temperature's time series of every single weather station (Sánchez-Benítez et al., 2017). The selection criterion adopted was established to maintain as much as possible consistent trends in climatic variation in time. The reduced datasets from each weather station was averaged in order to get October-March precipitation and Spring mean minimum temperature. The coefficient of variation of the precipitation

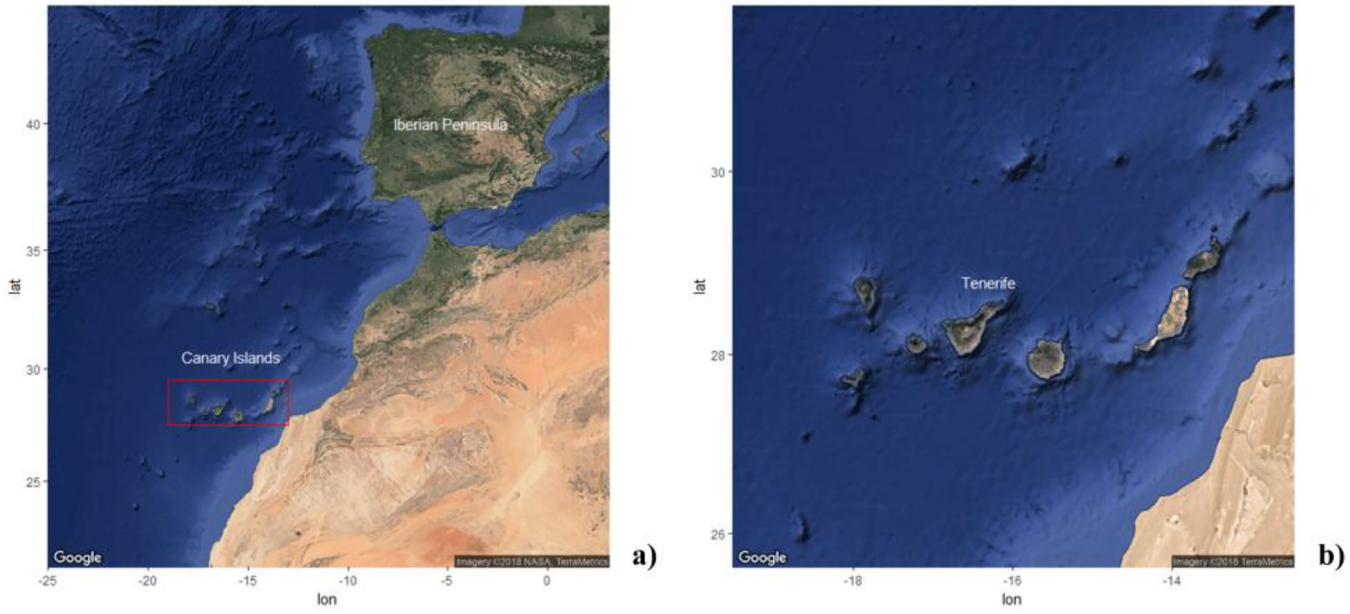

Fig. 1. (a) Canary Islands and (b) position of Tenerife island within Canary archipelago.

and the standard deviation of the temperature were also determined as a proxy of precipitation and temperature seasonality, using the methodology described in Hijmans (2004). These punctual climatic data were then used to create island-specific climatic surfaces by means of a co-Kriging procedure, using the elevation as covariate (Myers, 1984; Wilson and Silander, 2014) and the R package "*geoR*" (Ribeiro and Diggle, 2001). Road kernel density, calculated on the road network using 10 km regularly distributed sample points, was used here as a proxy of human disturbance and as a source of propagule pressure (Bacaro et al., 2015). All derived variables were calculated using the same grid of ASR (500 × 500 m resolution).

3.3. Data analysis and modelling

Spatial autocorrelation was evaluated calculating the Moran's I index using package "*spdep*" (Bivand and Piras, 2015) and the collinearity among the predictors was investigated through Spearman's rank correlation coefficient: predictors resulting with a Spearman's *rho* > |0.7| were excluded from the modelling procedure (Dormann et al., 2013). Once SAC was explored and the set of orthogonal predictors selected, a GLM was computed using ASR (response variable) as a function of the non-collinear covariates descripted above. This non-spatially explicit model was used as a baseline for comparison with the GLSM, and only the variables with nominal p-values < 0.05 were then added to the spatially explicit model (Diggle and Giorgi, 2016).

By definition, the GLSM is a generalized linear mixed model in which the random effects were derived from a spatial process. The Bayesian approach allowed 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 was formalized through prior distributions.

To take into account the spatial correlation of count data (e.g. ASR), a BGLSM using the Langevin-Hastings Markov Chain Monte Carlo (MCMC) algorithm was computed using the "*geoRglm*" R package (Christensen and Ribeiro, 2002). A strong-informative prior distribution (Rocchini et al., 2017) was then specified based on the spatial autocorrelation structure of the data, thus model predictions remain essentially data driven but accounting for spatial autocorrelation. MCMC simulations were run specifying 30,000 iterations, burn-in period of 8000 iterations and a thinning rate of 50. Chain diagnostics (e.g. autocorrelation) were visually inspected through "*coda*" R package (Plummer et al., 2006).

3.4. Model validation

75% (3929 grid cells, training dataset) of the entire response variable was randomly selected using "*sample*" R function and used to train the model, while the remaining 25% (1310 grid cells) was taken apart for testing the final prediction (validation dataset). For both models, predictions error estimate was calculate using a leave-one-out cross validation. Following Wilson and Silander (2014), the model was validated using two independent approaches: the median posterior predictions were compared with the observed data of (*i*) the training dataset and (*ii*) the validation dataset, in order to assess the predictive accuracy using the R^2 statistic, Root Mean Square Error (RMSE) and Mean Absolute Error (MAE). Both RMSE and MAE are in the same scale as the response variable and these statistics were calculated also for the GLM. All the analyses were performed using the R 3.4 environment (R Core Team, 2017) and the all the R scripts used are available in the supplementary materials section.

4. Results

Alien species mean richness was 4.18 species per cell (min. 1 and max. 27; Fig 2). The most common species on the island were *Opuntia maxima* Mill. (3161 occurrences), *Ageratina adenophora* (Spreng.) R. M. King and H. Rob. (2239 occurrences) and *Ricinus communis* L. (1615 occurrences).

SAC in the distribution of ASR values was confirmed by the significant Moran's Index value ($I = 0.873$, $P < 0.001$). Furthermore, the predictors Spring mean minimum temperature and Spring minimum temperature seasonality resulted highly correlated to Elevation (Spearman's *rho* = 0.85 and −0.97, respectively) and were then excluded from the analysis. Fig. 3 showed selected predictors' interpolated surfaces used to compute GLM and BGLSM estimates across the whole Tenerife Island. The two models showed different characteristics: the GLM's estimates showed a positive relationship between ASR and Road Kernel density and October-March Precipitation; in contrast, the other two predictors showed a slightly negative trend (Table 1). Compared to the GLM, the BGLSM estimated higher coefficients' values while the sign of the relationship remained except for precipitation

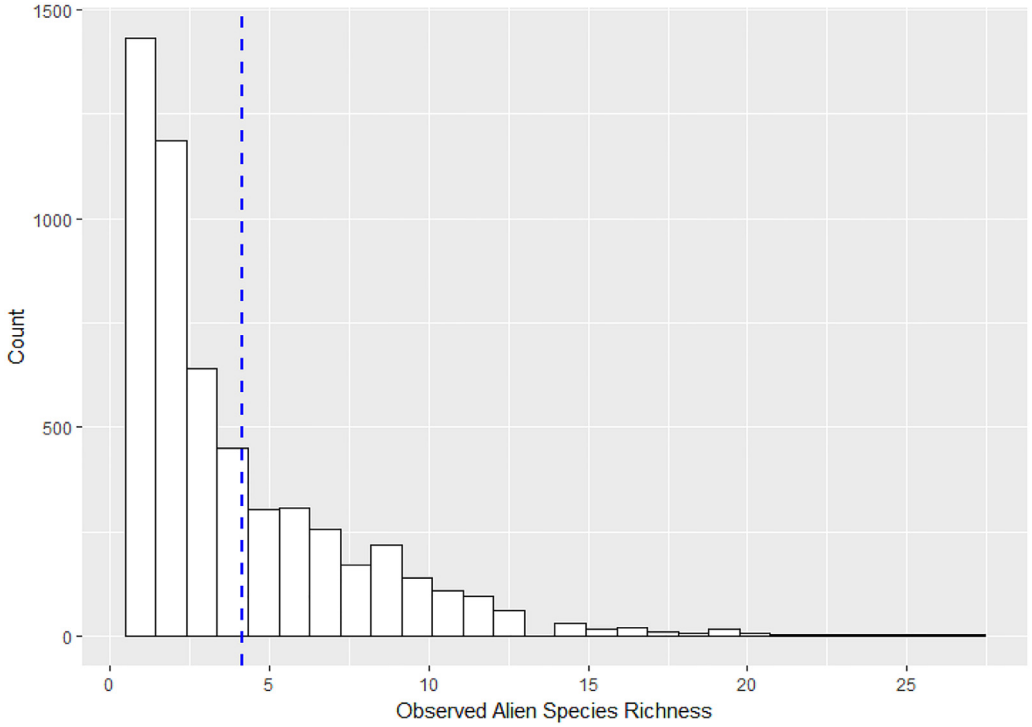

Fig. 2. Histogram representing the count of Alien Species Richness in Tenerife Island. The blue dashed line displays the mean value.

seasonality that showed a slightly positive estimate.

Including SAC in the model structure provided a consistent improvement in general model performance (ΔAIC = 4423, final AIC = 14,793) as well as a reduction of the predicted error estimated by the cross validation (Table 2). Moreover, the BGLSM showed also a better predictive accuracy performance for both calibration and validation datasets compared to the GLM, where BGLSM's RMSE and MAE are lower and R^2 was higher when compared to the GLM (Table 3).

Models outputs were summarized in Table 4. Both models have similar median values but GLM's predictions showed a narrower range of values compared to BGLSM, which predicted values closer to the observed values. On average, both models predicted higher ASR in the northern part of the island, consistently also with the location of the biggest cities (Santa Cruz de Tenerife on the eastern coast, Puerto de La Cruz on the N-W coast; Figs. 4, 5b). However, GLM output appeared smoother than BGLSM's one, suggesting that the latter better predicted ASR spatial patterns. In particular, the BGLSM highlighted as suitable areas the humid zones below 1000 m a.s.l, especially on the windward aspect.

Furthermore, a decreasing altitudinal trend in ASR was also observed, with higher values of ASR near the coastline and lower values above 1500 m a.s.l. Fig. 5d showed the uncertainty in the predicted ASR values. The model showed generally low uncertainty values but areas with higher uncertainty are clustered together, as Teide's area that shows the highest prediction uncertainty.

5. Discussion

5.1. Model performance

The incorporation of the spatial autocorrelation allowed us to build a reliable ecological model to understand ASR distribution on Tenerife (Fig. 5b). The outcomes of the model developed largely agree with previous studies indicating ASR strongly influenced both by natural and anthropogenic factors (Arévalo et al., 2005, 2008; Arteaga et al., 2009; Bacaro et al., 2015).

Nevertheless, ΔAIC suggested that incorporating SAC into a GLM framework allowed a consistent improvement in general model performance and predictions; in addition, the Bayesian framework here adopted allowed the derivation of predictions along with their associated uncertainty. The contribution of the prior and the data to the posterior distribution depends on their relative precision, we used a strong prior based only on the spatial autocorrelation structure of the data and not on the predictors' coefficients, thus allowing our model predictions to remain essentially data driven while accounting for spatial autocorrelation. The BGLSM showed a good predictive accuracy performance (Table 3), in agreement with Wilson and Silander (2014), which found congruous results using a similar Bayesian approach to obtain interpolated climate surfaces. Adding SAC into the modelling structure allowed the BGLSM to get better goodness of fit performances on both training and validation datasets, compared with the performances obtained by the GLM. As a consequence, the quality of the information derived was higher in terms of lower error rates and more accurate estimates, since it was clearly demonstrated how ignoring SAC could lead to biased parameter estimates (Kühn, 2007). Similarly, Bacaro et al. (2016) developed spatially-explicit rarefaction curves (SERs) which take into account the adjacency of the sampling units and, as a consequence, the spatial structure of the data, showing that not considering the data's spatial structure may lead to biased results when using classical rarefaction curves (Chiarucci et al., 2009). The inclusion of spatial information into modelling framework has gained a pivotal role also in community ecology (see Dray et al., 2012 for a review on this topic). Indeed, to analyze spatial patterns with multivariate data new methods such as distance-based Moran Eigenvector maps (dbMEMs or eigenfunction-based spatial analysis) were developed (Dray et al., 2006; Peres-Neto and Legendre 2010). These methodologies are based on eigenvector decomposition of connectivity matrices and Mantel correlograms (Borcard and Legendre 2012), which assess changes in the intensity of spatial patterns in a community at different lag-distances. In fact, the presence of spatial structures present in species assemblage may be the result both of neutral processes such as dispersal or biotic interactions among species (e.g. competition).

Concerning uncertainty, it resulted quite uneven distributed across the study area. Accordingly, our model showed areas with higher

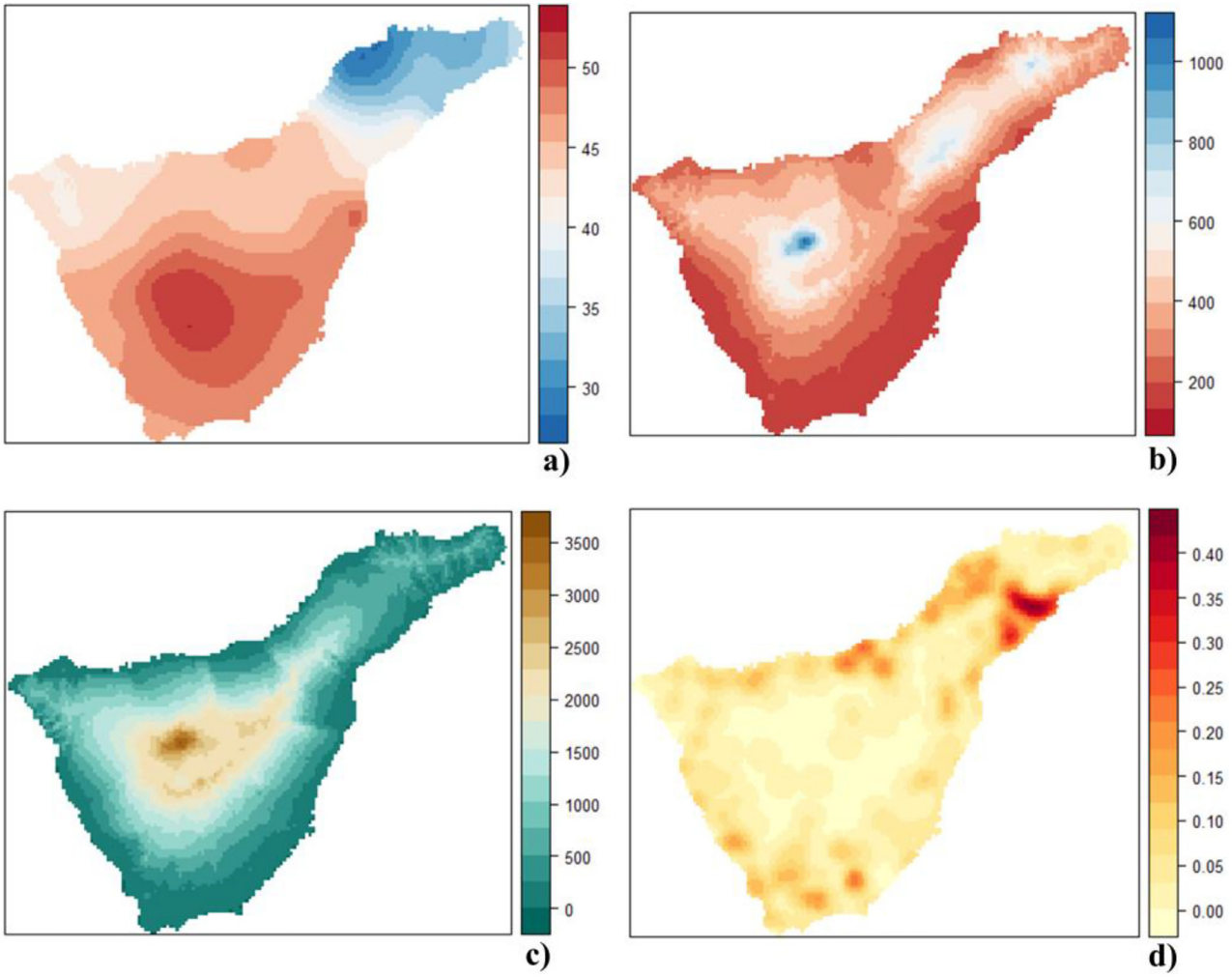

Fig. 3. Interpolated surfaces of the non-collinear predictors used in the model calculated via co-kriging procedure: (a) precipitations seasonality;(b) October–March precipitations; (c) Elevation; (d) Roads kernel density.

Table 1
Predictor coefficients for GLM, BGLSM and spatial parameters derived from the maximum likelihood analysis: τ^2 is the nugget (it represents variation at small scale), σ^2 is the sill (it represents the semi-variance of the variable), Φ is the range (it represents the distance limit beyond which the data are no longer correlated). For further details on these spatial metrics see Diggle and Ribeiro (2007).

Variables	GLM coefficients	BGLSM coefficients
Roads 10 km kernel density	0.202	3.855
Elevation	−0.472	−1.265
Precipitation seasonality	−0.028	0.003
October–March Precipitation	0.333	1.475
τ^2	–	0
σ^2	–	9.963
Φ	–	2.483

Table 2
Models leave-one-out cross validation results.

Model	Log.likelyhood	AIC	Prediction error
GLM	−9603	19,216	10.05
BGLSM	−7389	14,793	1.79

Table 3
Descriptive statistics of model performance. MAE = Mean Absolute Error; RMSE = Root Mean Square Error, R^2 = Coefficient of determination.

Model	Data%	MAE	RMSE	R^2
GLM	*75% training data*	2.62	3.36	0.29
	25% validation data	2.6	3.35	0.28
BGLSM	*75% training data*	0.14	0.38	0.99
	25% validation data	0.93	1.53	0.86

Table 4
Descriptive statistics of model outputs for BGLSM (posterior median and uncertainty) and GLM prediction.

	Median	Min	Max
Posterior median	3.09	0.64	27.24
Uncertainty	5.65	0.62	651.65
GLM	3.81	1.26	19.87

uncertainty clustered mostly in coastal areas and in Teide National Park, probably due to the lack of alien species data (and occurrence) at those elevations. At low-elevation costal zones, uncertainty metric reflects the complexity of landscape topography highlighting those heterogeneous areas where human-related land uses mainly occur (Fernández-Palacios and de Nicolás, 1995; Rocchini et al., 2018).

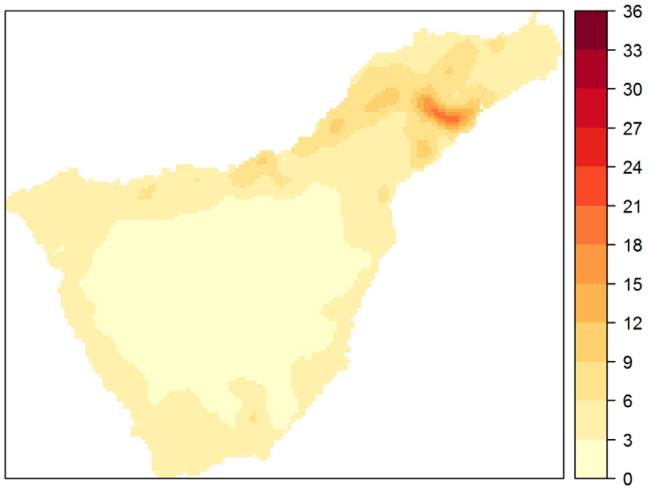

Fig. 4. GLM's Alien Species Richness predictions.

Furthermore, in a relatively restricted space such as Tenerife Island (Fig. 4), there is still considerable uncertainty in the predictions meaning that there is sparseness in the data and further sampling efforts are necessary.

5.2. Ecological implications

The Canary Islands and Tenerife in particular, are characterized 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).

In general, mild environmental conditions along with high humidity, low thermic and hydric stresses, and high productivity are largely responsible for quick establishment and dispersal of alien species on these islands (Whittaker and Heegaard, 2003). Concerning Tenerife, Arteaga et al. (2009) reported that these favorable conditions were found at about 800 – 1000 m a.s.l. whereas Arévalo et al. (2005) observed the highest number of both native and alien species. Accordingly, our model highlighted as suitable areas the humid zones below 1000 m a.s.l, especially on the windward aspect, due to the negative relationship between temperature and elevation. ASR was inversely related with elevation, as already observed in other studies (Arévalo et al., 2005; Arteaga et al., 2009; Bacaro et al., 2015). In fact, at higher elevations, thermic and hydric stresses reduce the number of

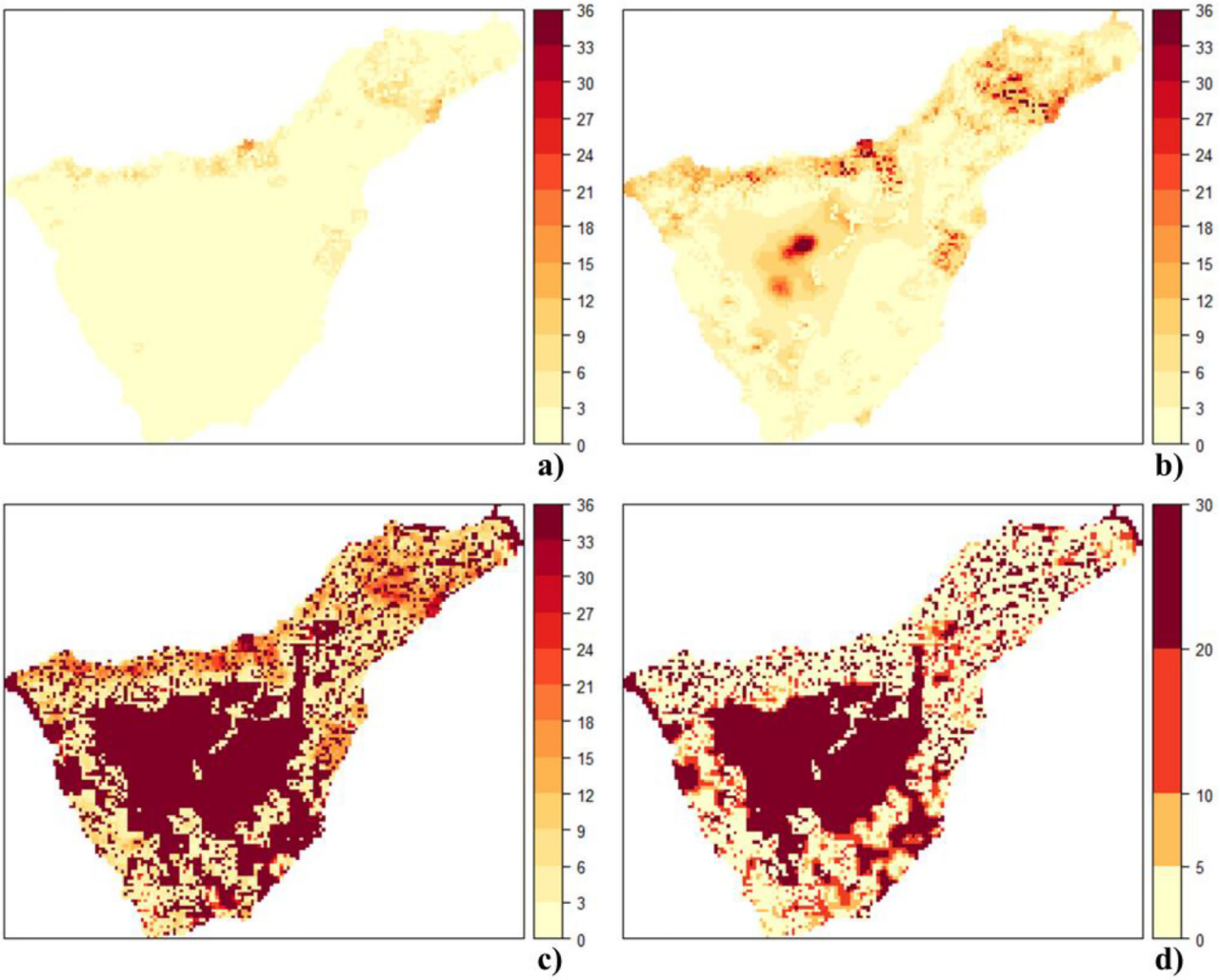

Fig. 5. BGLSM's Alien Species Richness predictions: (a) 2.5% quantile, (b) median, (c) 97.5% quantile, (d) uncertainty. Uncertainty of predicted Alien Species Richness. Values > 30 were included in the last color class to facilitate the understanding of the map.

successful colonization of alien species in different regions of the world (Fernández-Palacios, 1992; Alpert et al., 2000; Godfree et al., 2004; Pauchard and Alaback, 2004; Becker et al., 2005). Moreover, Barni et al. (2012) reported that in alpine continental area alien species remained below 1400 m a.s.l. reflecting the lack of alien flora of species pre-adapted to high elevation and to low temperatures. Regarding precipitation seasonality, Prevéy and Seastedt (2014) showed how precipitation seasonality could promote alien species spread, negatively affecting native plant community composition and phenology.

Roads are considered as one of the main pathways of alien species introduction and spread (Parendes and Jones, 2000; Pauchard and Alaback, 2004; Dietz and Edwards, 2006). The kernel road density estimation showed a clear positive relationship with ASR. Road density has increased especially in low to mid elevation belts of the Canary Islands, strictly associated to urban sprawl. In Tenerife, the road network (primary and secondary roads) occupies 3% of the total area (Otto et al., 2014). Hence, higher road density can be related to increased propagule pressure which is one of the most important factors explaining richness in alien species invasion success (Benedetti and Morelli, 2017). Generally, roadsides are characterized by environmental conditions and disturbances that differ substantially from those found in the habitats in their proximity (Trombulak and Frissell, 2000), thus resulting in road-specific plant communities (Bacaro et al., 2015).

6. Conclusions

In this study, a BGLSM was built in order to incorporate SAC and compared to a classic GLM to predict the spatial distribution of ASR in Tenerife Island. The comparison pointed out that the BGLSM performs better both in terms of goodness of fit and uncertainty pattern of the model prediction. Geostatistical models allow for the incorporation of information of environmental co-variation and neighborhood effects (Kreft and Jetz, 2007), improving the quality of predictions and getting an estimation of the response errors (Hoeting, 2009; Kühn et al., 2009), thus providing an useful tool to suggest how and where sampling activities should be performed. We further highlighted the importance to consider spatial autocorrelation and researcher's prior knowledge to increase the predictive power of statistical models. These models and associated uncertainty may serve as essential management tools highlighting those portions of territory that will be more prone to biological invasions and where monitoring efforts should be addressed. Unlike disease biogeography where these geostatistical approaches are widely applied (e.g. Patil et al., 2011), we advocate their application in the field of spatial ecology due to their capability to provide more reliable parameter estimates.

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Supplementary materials

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