










## RESEARCH ARTICLE

# Biogeographic origins and drivers of alien plant invasions in the Canary Islands

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**Funding information**

Fundación BBVA, Grant/Award Number: INVASION - PR19\_ECO\_0046; Spanish Ministry of Science and Innovation, Grant/Award Number: ASTERALIEN - PID2019-110538GA-I00; Juan de la Cierva-Formación Fellowship, Grant/Award Number: FJC2020-046353-I; Ramón y Cajal Program, Grant/Award Number:

**Abstract**

**Aim:** Understanding the historical and contemporaneous drivers of invasion success in island systems can decisively contribute to identifying sources and pathways that are more likely to give rise to new invaders. Based on a floristic-driven approach, we aimed at determining the origins of the invasive alien flora of the Canary Islands and shedding light in the mechanisms shaping their distribution within the archipelago.

**Location:** Canary Islands.

**Taxon:** Vascular plants.

**Methods:** An updated checklist of the invasive alien flora of the Canary Islands was assembled along with complementary information related to the native biogeographical regions, stage of invasiveness and dates of naturalization. Statistical models were employed to describe differences in the number of species over space and time. We also used multivariate techniques to evaluate competing hypotheses related to the mechanisms driving invasive floristic composition within the archipelago.

**Results:** We provided a list of 149 alien plant species with a certain degree of invasiveness. The greatest number of invasive species originated from the Neotropics followed by the Cape Region, tropical Africa and the Mediterranean Basin. We observed a slow but steady increase in numbers of invasive species until the 1950s, followed by a stronger rise thereafter. In order to explain composition dissimilarity of the invasive flora among islands, a climatic matching hypothesis was fully supported, with geographic isolation and contemporary human-mediated connectivity hypotheses receiving less and null support respectively.

**Main Conclusions:** We showed that the Neotropical region is the main source of plant invasions to the Canary Islands, outnumbering those from other regions with a Mediterranean-type bioclimate. The assembly of the invasive flora within the archipelago appears to be driven primarily by climate, but with geographic distance also

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RYC-2016-20506; Academia Canaria de Investigación Gobierno de Canarias FPI 2021 Fellowship, Grant/Award Number: TESIS2021010101

Handling Editor: Daniel Chapman

playing a role. This study calls for archipelago-dependent assessments of the underlying mechanisms that contribute to plant invasion success within insular systems.

#### KEYWORDS

climatic matching, floristic assembly, geographic distance, invasive alien species, island biogeography, Mediterranean climate type, naturalized species, transport networks

## 1 | INTRODUCTION

Global trade, transport and horticulture have become driving forces promoting human-assisted dispersal of plant species across oceanic and continental regions (Capinha et al., 2015; van Kleunen et al., 2020). As a consequence, an increasing number of species have been introduced beyond their native ranges, with a fraction naturalized by forming self-replacing populations in natural or human-made habitats (naturalized alien species sensu Lambdon et al., 2008; Pyšek et al., 2004). A subset of these naturalized alien species has also become invasive (invasive alien species sensu Lambdon et al., 2008; Pyšek et al., 2004), emerging as important drivers of global change and species extinctions (Bellard et al., 2016; Bellard et al., 2017; Russell & Kueffer, 2019).

The number and origins of invasive alien plant species vary across spatial and temporal scales depending on several interacting factors, including history and timing of human transport pathways, geographic isolation and distance, abiotic conditions and species traits (Capinha et al., 2015; Irl et al., 2021; Kusumoto et al., 2021; Monnet et al., 2020; Moser et al., 2018; van Kleunen et al., 2015). Consequently, different underlying mechanisms of biological invasion have been proposed (Catford et al., 2009; Di Castri, 1989; Theoharides & Dukes, 2007). Among them, the 'climate matching' hypothesis (Richardson & Thuiller, 2007; Thuiller et al., 2005), which postulates that alien species are most likely to establish in areas that are climatically similar to their native range, has received mounting evidence (e.g., Cao Pinna et al., 2021; Capinha et al., 2015; Monnet et al., 2020). Recently, Yang et al. (2021) showed that the level of floristic homogenization due to plant introductions increases with climatic similarity, even among geographically distant regions.

Floristic homogenization of invasive alien floras among regions can be further fostered by historical or current administrative relationships due to enhanced intensive trade and transport (Yang et al., 2021). Indeed, anthropogenic introductions can be highly asymmetric and substantially related to the history of human occupation and trade networks (Hulme, 2015; Monnet et al., 2020; Turbelin et al., 2017). From the 15th to the early 20th century, European imperialism expanded, displacing and replacing not only native societies but also their biotas (Di Castri et al., 1990; Simberloff, 2004). The historical legacy of these trade and political relationships led to the development of the 'Imperialist Dogma' hypothesis (Crosby, 2004). This hypothesis proposes that, due to human colonization history, Old World European species have spread more frequently and widely outside their native ranges than New World species (Di Castri, 1989;

Pyšek, 1998). Contemporary global trade still has its roots on the historical legacy of the European imperialism, which perpetuates trade patterns in many geographic regions (Gokmen et al., 2020). Accordingly, van Kleunen et al. (2015) have shown that continents in the Northern Hemisphere have been key sources of alien species to all other continents, with North America accumulating the largest number of non-native plants. Eurasian species were proposed to be at clear advantage everywhere (van Kleunen et al., 2015) because of their long coevolution with humans and their disturbance regimes (Jeschke & Strayer, 2005; Kalusová et al., 2017; Monnet et al., 2020). The main European sources of alien plant species have included regions such as the Mediterranean Basin (Fridley, 2008) in general, and the Iberian Peninsula in particular (Casado et al., 2018).

The geographic origins of invasive alien plants have been shown to be different when time periods related to important socio-economic events are considered. For instance, evidence points to the rising importance of extra-European regions as sources of alien species, in parallel with the development of emergent economies and global increase in trade activity (Seebens et al., 2015). This pattern is contrary to the 'Imperialist Dogma' and seems to have globally emerged 60 years ago with the globalization of anthropogenic transport networks (Seebens et al., 2015). In fact, it has been increasingly shown that socio-economic variables, such as trade networks, can be as (or even more) important drivers of plant invasion as climate similarity and geographic distance (Chapman et al., 2017; Essl et al., 2019). Nonetheless, increased residence time on a given region and limited geographic distance among invaded and non-invaded areas within that region can increase the probability of alien plant naturalization and invasion (Lambdon et al., 2008).

Despite the importance of studying source-sink dynamics in order to gain insights related to spatial and temporal invasiveness patterns (Fridley & Sax, 2014; Kusumoto et al., 2021; Visser et al., 2016), the main sources of invasive alien floras remain unknown and controversial for many regions (Fridley, 2008; Pyšek, 1998). This is particularly true for many insular systems (Lenzner et al., 2020; Patiño et al., 2017), which calls for regional assessments of the major forces for ongoing biotic homogenization of island floras (Otto et al., 2020).

Here, we investigate the origins of the invasive alien vascular flora of the Canary Islands to determine which biogeographic regions have played a dominant role as sources of invasion. Fox (1990) proposed that the five Mediterranean-climate regions (Mediterranean Basin, California, central Chile, South Africa and south-western Australia) have exchanged significant numbers of invasive plant species, but with the Iberian Peninsula as the main source to the

other regions (Casado et al., 2018). In addition, it is expected that plant species from other Mediterranean-climate regions, largely preadapted to these environments, would have a higher probability of naturalization and spread across the Mediterranean Basin (Cao Pinna et al., 2021; Casado et al., 2018). We anticipate that such phenomena should have left an important imprint in the Canary archipelago, which is in general characterized by both strong climatic similarity and floristic relationships with the Mediterranean Basin (del Arco-Aguilar & Rodríguez-Delgado, 2018).

The Canary Islands exhibit very contrasted features in terms of geological history, topographical complexity and associated climatic gradients. Such differences help to explain the broader array of ecosystem types found on the highest islands compared with the lowest ones (from arid and semiarid coastal scrubs, through semiarid thermophilous woodlands, montane cloud laurel forests and xeric pine forests to summit scrub). Thus, the western and central islands are characterized by high, complex topographies, relatively humid climates and a full range of ecosystem types, while the eastern ones are flatter, drier and less ecologically diverse (del Arco-Aguilar et al., 2010; del Arco-Aguilar & Rodríguez-Delgado, 2018). For at least 2000 years, these zonal ecosystems have been subject to anthropogenic pressures and even more so following the European conquest in the 15th century (de Nascimento et al., 2020). The level of human occupation, land use history and transportation network also vary depending on the island, with human pressure decreasing from the central islands to both the easternmost and westernmost edges of the archipelago. We also investigate the relative importance of geographic, climatic and transportation factors in shaping the within-archipelago composition of the invasive flora.

Specifically, we test the four following hypotheses:

**'Imperialist Dogma' Hypothesis (H1):** Following the 'Imperialist Dogma', the Mediterranean Basin has been the prevalent source of invasive alien plants to the Canary Islands, given its strong macroclimatic matching, long-term commercial exchange and relatively short geographic distance to the archipelago.

**Naturalization Rate Hypothesis (H2):** Rates of first introduction and naturalization should have increased in recent years, when global trade has peaked (Hulme, 2009; Seebens et al., 2017). Furthermore, the rates of naturalization from specific biogeographic regions are expected to differ when the colonial times (i.e., 1500–1900) are compared with more recent times (i.e., last 50 years), when predominant routes of human migration through the Canary Islands have changed.

**Within-archipelago Climate Matching Hypothesis (H3):** Following the climate matching hypothesis, insular floras within a given archipelago should converge towards more similar assemblages of invasive species with increased climatic similarity. The Canary islands of Lanzarote and Fuerteventura are much flatter and drier than the central and western islands. Thus, we expect greater floristic similarities among environmentally similar islands.

**Enhanced Connectivity Hypothesis (H4):** It is plausible that the positive correlation observed between trade volumes and invasion patterns at the global scale (Chapman et al., 2017; Seebens

et al., 2015) can exhibit a similar correspondence at the regional scale (Hulme, 2021). Under such an assumption, the explanatory power of current interisland transport networks for compositional dissimilarity of invasive floras within the Canary archipelago should parallel that of climatic similarity and geographic distance among islands.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The Canary Islands, a volcanic archipelago situated in the north-eastern Atlantic Ocean, is one of the most biodiverse oceanic insular systems of plants on the planet (Patiño et al., 2014), being one of the most relevant hotspots of plant biodiversity within the Mediterranean Basin (Médail & Quézel, 1999). The Canary archipelago not only exhibits high levels of endemism (539 vascular plants which means almost 40% of the native flora) but also of alien species (del Arco-Aguilar & Rodríguez-Delgado, 2018). The archipelago is characterized by a general subtropical Mediterranean climate with strong gradients in temperature and precipitation depending on elevation, topography and longitude (del Arco-Aguilar et al., 2010). In addition to the elevational zonation (del Arco-Aguilar & Rodríguez-Delgado, 2018), the archipelago exhibits a strong precipitation gradient from west to east, with the western islands much wetter than those to the east (Sánchez-Benítez et al., 2017). The Canary archipelago was first colonized by humans, from North Africa, during the first millennia CE (Fregel et al., 2019), and then subsequently by the Castilian conquest during the 15th century AD. As a result, an important increase in trade and land use transformation caused a significant reduction of the main zonal vegetation types as well as a noteworthy increase in the introductions of alien plants (del Arco-Aguilar & Rodríguez-Delgado, 2018). Since Castilian colonization, the archipelago has been a crossroad of several intercontinental trade routes (Bosa, 2004; James, 1985; Santana-Pérez, 2018), which makes it challenging to track the origins of alien plant species.

### 2.2 | Information sources

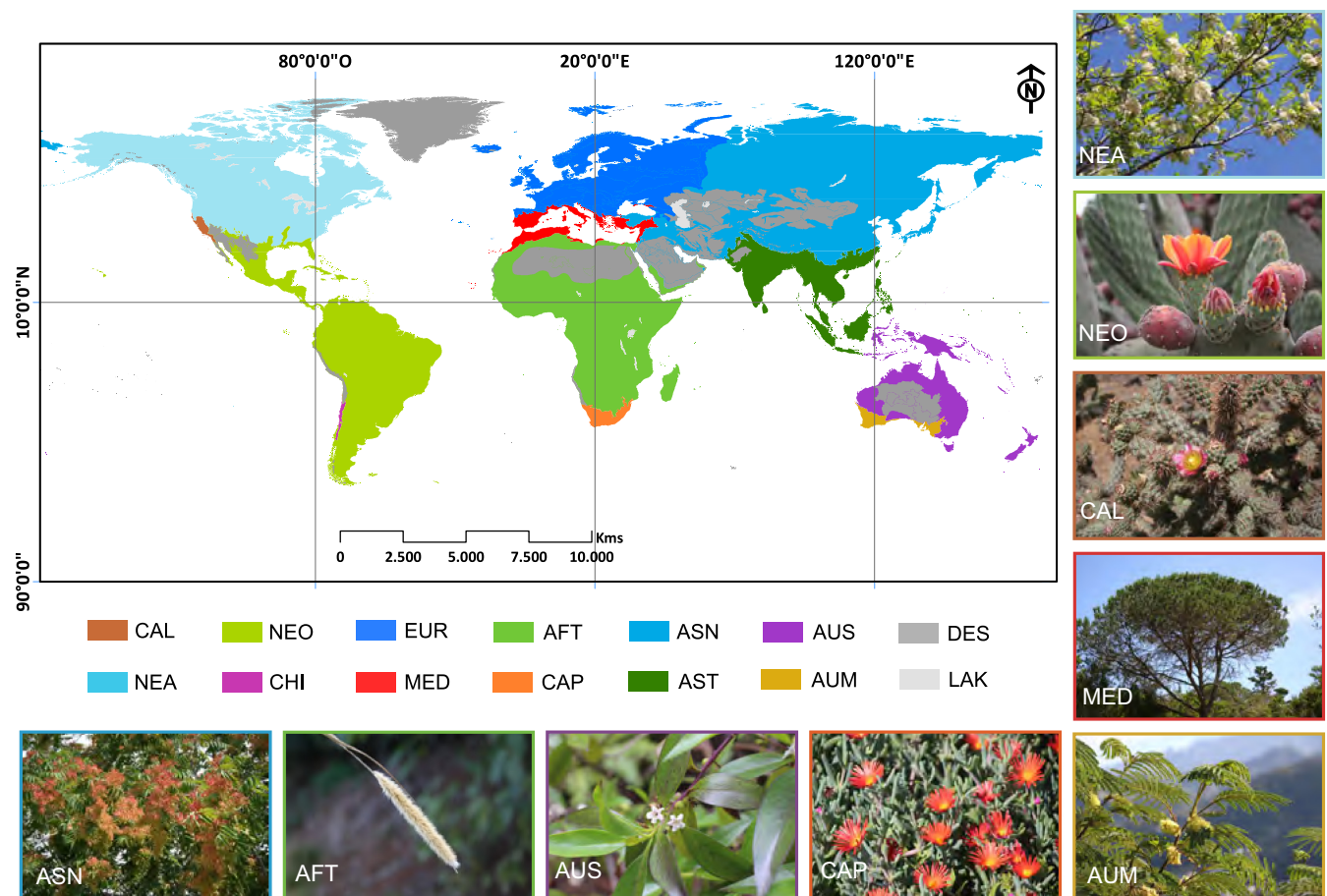
A thorough search of primary and secondary references, including the web database BIOTA (<https://www.biodiversidadcanarias.es/>) and other sources of information, such as peer-reviewed indexed and non-indexed journals, technical reports, books and other publications, allowed us to obtain an up-to-date checklist of the invasive alien plant species of the Canary Islands. In order to refine the list, we first excluded species records which we could not confidently delineate a precise geographic native range. Following the approach proposed by Pyšek et al. (2004), widely cultivated species across the archipelago were also discarded due to the idea that the environmental and anthropogenic factors that shape their distributions are likely to be different from those of non-cultivated alien species (Monnet et al., 2020). As proposed by Capinha et al. (2015), we also

discarded all records for which, according to BIOTA, the invasiveness or alien status was mentioned as uncertain (e.g., probable invasive, probable alien). In total, we used approximately 64 data sources (Appendix S1). The scientific names of species were standardized with global (Plants of the World Online, <http://www.plantsoftheworldonline.org/>) and regional (BIOTA) databases.

We then classified each alien species as naturalized or invasive following the framework proposed by Blackburn et al. (2011), which relies on the magnitude and irreversibility of their negative ecological impacts. The statistical analyses were performed for the group of invasive alien species separately, and for the invasive and the naturalized groups together (see Statistical analyses).

Next, we compiled information regarding the native geographic range of each alien species (see Appendix S1 for the complete list of references used). We defined a set of biogeographic regions intended to represent the native areas for the human-mediated introduced diaspores (Figure 1). Biogeographic regions were thus demarcated

following Takhtajan (1986), Cowling et al. (1996) and Cox's (2001) works, as follows: (A) the five regions with a Mediterranean-type climate separately, including, the Mediterranean Basin, Cape Floristic region, California Floristic Province, central Chile and south-western Australia (Cowling et al., 1996); (B) Palearctic Europe, excluding the Mediterranean Basin; (C) North America as Nearctic, excluding the California Province; (D) Neotropics which extends from tropical regions of Mexico through Central America and into South America, the Galapagos and the Revillagigedo archipelagos, but excluding central Chile; (E) Tropical Africa, excluding the African areas of the Mediterranean Basin and the Cape region; (F) Palaeartic East Asia, including non-tropical areas of Asia from the Palearctic; (G) Indo-Malayan or tropical Asia, including tropical areas of south and southeast Asia and extends through the Malay Archipelago; (H) Australasia, which combines Australia and New Zealand into a single region following Cox (2001), and extends as far as New Guinea and Polynesia. A final category, including species extending across two



**FIGURE 1** Biogeographic regions defined to represent the source regions for the human-mediated introduced plant species into the Canary Islands. CAL, Mediterranean California; NEA, Nearctic region; NEO, Neotropical region; EUR, Palearctic Europe; MED, Mediterranean Basin including Europe, North Africa and Middle East; AFT, Tropical Africa; CAP, Cape Region of South Africa; ASN, Palearctic Asia; AST, Tropical Asia; AUM, Mediterranean Australia; AUS, Australasia; DES, cold and hot (semi)deserts; LAK, lakes and inner seas. Mediterranean Chile is only highlighted in the map (see Methods). Examples of the best represented floristic regions in the invasive flora of the Canary Islands: NEA, *Robinia pseudoacacia* L.; MED, *Pinus pinea* L.; ASN, *Ailanthus altissima* (Mill.) Swingle; NEO, *Opuntia tomentosa* Salm-Dyck; AFT, *Cenchrus purpureus* (Schumach.) Morrone; AUS, *Myoporum laetum* G. Forst.; CAL, *Cylindropuntia prolifera* (Engelm.) F.M. Knuth; CAP, *Malephora crocea* (Jacq.) Schwantes; AUM, *Paraserianthes lophantha* (Willd.) I.C. Nielsen. A version of the figure suitable for colour blindness is provided in Supporting Information.



or more of the aforementioned regions (widespread), was defined but not considered in the subsequent analyses due to the impediment for addressing signals of macroclimatic similarity and the lack of a predominant biogeographic pattern.

### 2.3 | Time of introduction and naturalization

Data on the first year of record (i.e. species introduced associated with anthropogenic environments such as gardens and urban areas) and naturalization (i.e. species spontaneously growing and reproducing in the wild) in the Canary Islands for each alien species were gathered from several information sources including personal observations (Appendix S1). Following Seebens et al. (2017), when records of time shorter than 10 years were provided, a year within the specified range was randomly selected to avoid arbitrary peaks at, for example, the mean value of the ranges. Records of time periods longer than 10 years were not considered for the subsequent analysis. We restricted the analysis to species introduced after 1500 due to the lack of data prior the conquest of the Canary Islands by Europeans that finished in 1496 (Fregel et al., 2009).

### 2.4 | Characterization of islands

Three mechanisms that can govern floristic dissimilarities of alien floras among oceanic islands were tested, including climatic similarity, geographic distance and recent connectivity by human transportation (see Statistical analyses). To assess climate similarity, we used climatic data at the finest resolution available (30 seconds) from WorldClim (Fick & Hijmans, 2017). After evaluating correlation between the 19 WorldClim variables and using a threshold of a Pearson's correlation coefficient  $r < |0.7|$ , we selected three variables with low correlation ( $r < |0.39|$ ): mean diurnal temperature range, temperature seasonality and precipitation seasonality. These three variables describe the level of seasonality of a given region, which have been identified as suitable proxies to explain plant invasion success in introduced ranges across Mediterranean-type regions (González-Moreno et al., 2015; Hierro et al., 2009). Geographic distances were calculated as the minimum distance following a straight line between each pair of Canary islands. The recent connectivity by human transportation was estimated considering regular connections between islands by air and sea. Data for the last 16 years (between 2004 and 2020) of commercial flights between island airports were obtained from the 'Instituto Canario de Estadística' (<http://www.gobiernodecanarias.org/istac/estadisticas/sectorservicios/>). Data from linear shipping connectivity were obtained from the current offer of the two linear shipping companies working on the archipelago (<https://www.fredolsen.es/es>; <https://www.navieraaromas.com/es>). The human transportation connectivity was estimated adding up information obtained from the two above-mentioned sources: (i) the average number of commercial flights per pair of islands per year; and (ii) the number of boat trips between each pair

of islands in a year. The inverse of this connectivity matrix ( $M^{-1}$ ) was used as a proxy for the cost or distance between islands by human transportation.

### 2.5 | Statistical analyses

To test the 'Imperialist Dogma' *Hypothesis* (H1) that Mediterranean climate regions in general, and the Mediterranean Basin in particular, have been predominant sources of invasive alien plants for the Canary Islands, we fitted generalized linear mixed models (GLMMs) with a Poisson distribution following a top-down strategy for model selection (e.g. Bunnefeld & Phillimore, 2012). Specifically, we used the number of invasive alien species from a particular region to a given island as the response variable, and the biogeographic origin as a predictor (fixed effect with 11 levels corresponding to each of the source regions). In order to test if the Mediterranean Basin has played a role in being a predominant source of invasive species, the Mediterranean region was set as the first level of the biogeographic origin factor. This allowed direct testing of deviations from zero of the estimators for the remaining biogeographic regions. First, the best random effect structure, with the biogeographic origin factor considered, was selected using the Akaike information criterion corrected for small sample size (AICc) approach (Burnham & Anderson, 2002). We ran models with and without a varying intercept across islands as a grouping variable (seven levels corresponding to each of the main Canary islands). A more complex model structure including a random slope of island did not converge. Second, after finding the best random effect structure, the importance of the fixed effect was evaluated using the same model selection procedure based on AICc and compared with a model only including an intercept. Models with  $\Delta AICc > 2$  relative to the best model were discarded, as they have less statistical support (Burnham & Anderson, 2002). We also used pairwise Tukey post hoc tests to check for differences in number of invasive alien species between biogeographical origins. The models were fit using 'glmmTMB' (Brooks et al., 2017) and 'mixlm' (Liland & Sæbø, 2022) R packages.

Generalized linear models (GLM) were used to investigate the relationship between the temporal dynamics of the naturalization and the trend of invasive alien species accumulations at the scale of the whole archipelago (*Naturalization Rate Hypothesis*, H2). The number of invasive alien species for a given period of 50 years and from a particular biogeographic region was set as the response variable following a Poisson distribution, and the naturalization time and the biogeographic source were the two predictor variables of these models. In order to accept the *Naturalization Rate Hypothesis*, a model including the two predictors should show a superior fit identified by AICc values, as it is expected that the accumulation rates and origins of the alien flora naturalized in the Canary archipelago has changed during the last 50–60 years. To determine the goodness of fit of the models, we calculated the adjusted amount of deviance ( $adjD^2$ ) accounted for (Guisan & Zimmermann, 2000). The  $adjD^2$  takes into account the number of observations and the number of

predictors, thus allowing direct comparison among different models. These analyses were performed using the R packages 'lme4' (Zeileis & Hothorn, 2002), 'ModEvA' (Barbosa et al., 2013) and 'AICcmodavg' (Mazerolle, 2020) in the R environment.

After their arrival and establishment, invasive alien species can spread across the archipelago, potentially establishing distinctive assemblages in each island. In order to describe floristic relationships among islands, we chose the weighted arithmetic average clustering method (WPGMA) derived from the UPGMA (unweighted), a clustering algorithm that has proved to perform well in biogeographic regionalization studies (Holt et al., 2013). To provide a complementary non-hierarchical description of floristic relationships, islands were plotted in a two-dimensional ordination using principal coordinates analysis (PCoA). Then, we used a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017) to compare differences in the species composition between the groups identified by the WPGMA and PCoA approaches; all these analyses were performed using the R package 'vegan' (Oksanen et al., 2020).

To investigate the correlation between several potential drivers and the variation in invasive alien plant assemblages across the Canary Islands (*Within-archipelago Climatic Matching* and *Enhanced Connectivity Hypotheses*, H3–4), we performed generalized dissimilarity models (GDM). The GDM approach accounts for the non-linearity of the relationship between floristic dissimilarity and distance in wide environmental and geographic gradients, considering the deviations from linearity along each individual abiotic variable. For that, several monotonic I-spline basis functions are linearly combined for each predictor, and pairwise differences among sites are calculated along this derived function. For distance-matrix predictors, the I-spline fitting is performed directly to the distances (Ferrier et al., 2007). A GDM was fitted using Jaccard floristic dissimilarities between islands as the response variable, and the geographical distance matrix, the human transportation cost matrix and three non-correlated untransformed environmental variables (diurnal temperature range, temperature seasonality and precipitation seasonality) as predictors. Correlations between predictor variables were assessed prior to analyses using the Pearson's rank correlation coefficient  $r$ . The criterion value of  $r$  to identify multicollinearity issues was set to  $r < |0.7|$  following Dormann et al. (2013). As all absolute values of  $r$  were  $< 0.5$ , we assumed there was no or very low multicollinearity. This model was then fit using the R package 'gdm' (Fitzpatrick et al., 2021) and the number of I-spline basis functions to fit each predictor in the model was left as default (three). We set 100 permutations to evaluate model and variable significance and estimate variable importance by using *gdm.varImp* function, in which a backward elimination process is implemented to drop the least important variable in each step, retaining in the model only significant predictors ( $p$ -value  $< 0.05$ ). The magnitude of floristic dissimilarity accounted for each predictor is given by the sum of coefficients of the fitted I-splines, and the rate of change along the gradient by the slope of the derived function (Ferrier et al., 2007). All the statistical analyses were repeated for the invasive and naturalized alien species groupings together (see Appendix S2).

## 3 | RESULTS

### 3.1 | The invasive alien flora of the Canary Islands

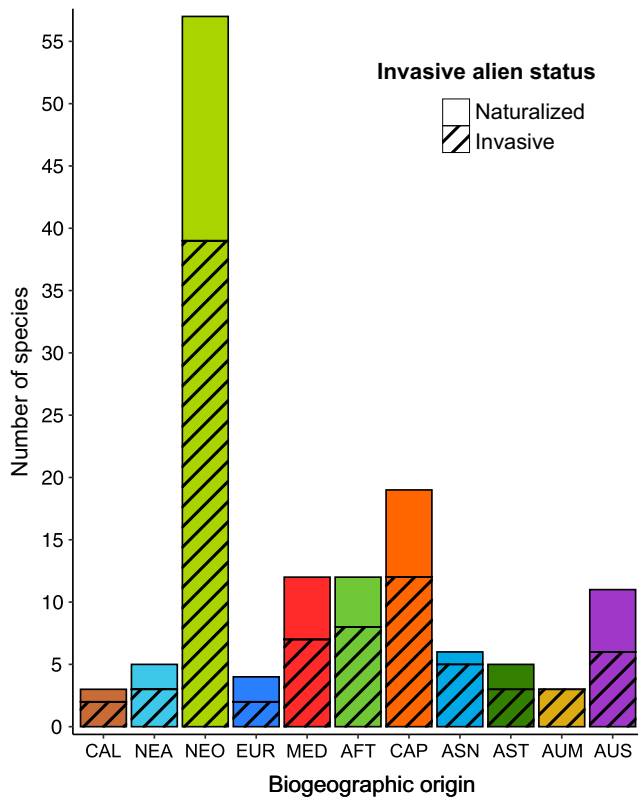
The updated list comprises 137 alien species with different levels of invasiveness: 90 invasive and 47 naturalized plant species. If widespread taxa are considered, there were 101 invasive and 48 naturalized species (Appendix S1). The families with the highest invasive alien diversity in the Canary Islands are Cactaceae (18 species), Poaceae (18), Asparagaceae (13) and Fabaceae (11), which account for 38.5% of the alien flora with a certain level of invasiveness. Genera such as *Agave*, *Opuntia* and *Cylindropuntia* had the highest number of species (Appendix S1). Around 39.4% were herbaceous species, while 61.6% were woody species, with only 16 tree species (Appendix S1). The highest number of invasive alien species is found on Gran Canaria (79 species) and Tenerife (78), while the lowest on Lanzarote (35) and El Hierro (31) respectively.

The distribution patterns of the two groupings of species (invasive vs. naturalized) are centred-skewed, with most species occurring in three or four islands ( $3.9 \pm 2.0$  for invasive and  $3.4 \pm 2.1$  for naturalized respectively). All the subsequent statistical analyses conducted in the present study that considered only invasive alien plants and both invasive and naturalized taxa showed a practically identical outcome (for comparisons, see Appendix S2). For this reason, hereafter, we only discuss the results for the grouping exclusively including invasive alien species.

### 3.2 | Native ranges of invasive alien plant species

The greatest number of invasive alien species was originated from the Neotropics (39 species), with Cape Region in South Africa (12), tropical Africa (8) and the Mediterranean Basin (7) displaying important complementary roles as sources to the Canary Islands (Figure 2). These four regions account for 73.3% of the invasive alien flora. When the proportion of each biogeographic region acting as a source of invasive alien species was estimated within each island, the pattern of an overrepresentation of species with a Neotropical origin followed by the Cape Region, tropical Africa and Mediterranean Basin was consistent across the archipelago (Figure 3).

According to the GLMM analyses, the best random effect structure consistently included a random intercept of island (Table S2.1), based on the  $\Delta AICc$  and  $AICc-w$ . Using this random structure, GLMM fits were substantially improved by including effects of the biogeographic region acting as a source, compared with a null model including only an intercept in the fixed structure (Table 1; see also Table S2.2). This result supports that the number of invasive species on each island substantially differs depending on their biogeographic origin. According to GLMM coefficient estimates and Tukey post hoc tests (Figure S2.1), the number of invasive plants was significantly higher in the Neotropical grouping compared with groups from a Mediterranean, Cape Region, tropical African and Australasian origins.

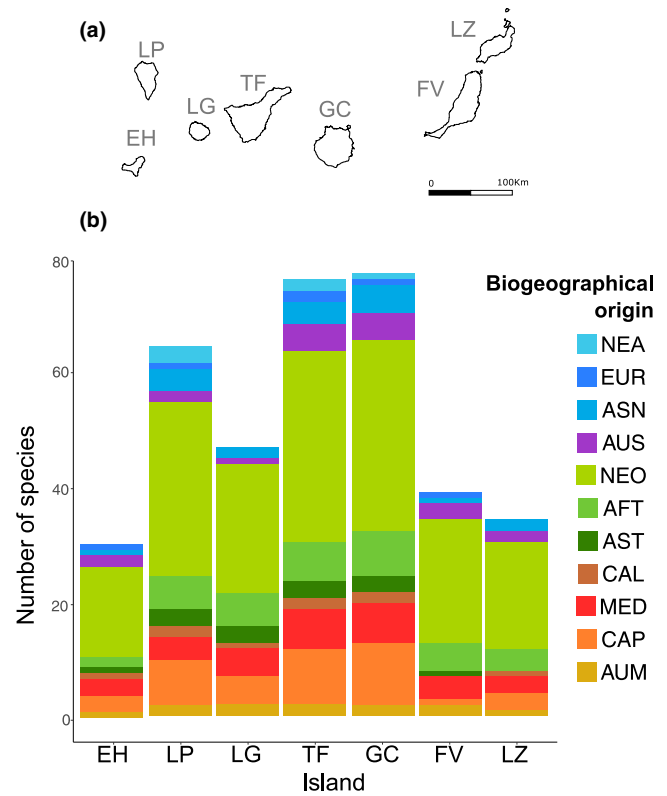


**FIGURE 2** Total number of invasive (and naturalized) alien plant species across the Canary Islands grouped according to the biogeographic origin. CAL, California; NEA, Nearctic; NEO, Neotropics; EUR, Palearctic Europe; MED, Mediterranean Basin including Europe, North Africa and Middle East; AFT, Tropical Africa; CAP, Cape Region of South Africa; ASN, Palearctic Asia; AST, Tropical Asia; AUM, Mediterranean Australia; AUS, Australasia.

### 3.3 | Timing of the first naturalization records

A pattern emerged in the first naturalization records of invasive plant species. This main pattern described slow but steady increases until approximately the 1950s, followed by stronger increases thereafter (Figure 4). This pattern is observed in all biogeographic groupings, with the exception of Californian species due to its recent record of naturalizations. We found statistical support for the influence of the naturalization time and biogeographic origin on the number of invasive alien species (model 3: time and biogeographic origin as predictors;  $\chi^2 = 53.85$ ,  $p$ -value =  $2.01 \times 10^{-08}$ ); being the amount of variance explained high ( $\text{adj}D^2 = 0.63$ ). The rest of the models had from a similar (model 1: time;  $\Delta\text{AICc} = 0.11$ ;  $\chi^2 = 37.81$ ,  $p$ -value =  $4.12 \times 10^{-07}$ ,  $\text{adj}D^2 = 0.42$ ) to an inferior fit (model 2: biogeographic origin;  $\Delta\text{AICc} = 18.73$ ;  $\chi^2 = 16.041$ ,  $p$ -value =  $2.96 \times 10^{-03}$ ,  $\text{adj}D^2 = 0.09$ ). The significance of the interaction between naturalization time and biogeographic origin could not be estimated because we did not have all the potential combinations for the two predictors across the whole series of 50-year periods.

We also considered the time since introduction (i.e. first record), with the goal of studying the role of residence time in determining



**FIGURE 3** (a) Geographic extent of the archipelago of the Canary Islands. LZ, Lanzarote; FV, Fuerteventura; GC, Gran Canaria; TF, Tenerife; LG, La Gomera; LP, La Palma; EH, El Hierro; (b) Bar plot showing the total number of invasive alien plant species per island and the relative contribution of the main biogeographical regions. CAL, Mediterranean California; NEA, Nearctic; NEO, Neotropics; EUR, Palearctic Europe; MED, Mediterranean Basin including Europe, North Africa and Middle East; AFT, Tropical Africa; CAP, Cape Region of South Africa; ASN, Palearctic Asia; AST, Tropical Asia; AUM, Mediterranean Australia; AUS, Australasia. A version of the figure suitable for colour blindness is provided in Supporting Information.

invasion success. Nonetheless, available information on the time since introduction was scarce ( $n = 51$ ), preventing us from achieving such a goal. The average difference between the time of introduction and the time of expansion was around 100 years ( $92.1 \pm 60.3$  years).

### 3.4 | Inter-island floristic relationships

The first PCoA axis separates the richer in number of invasive alien plants from the poorer islands, while the second PCoA axis supports three groupings (Lanzarote-Fuerteventura; El Hierro-La Palma-La Gomera; and Gran Canaria-Tenerife; Figure 5a). The WPGMA clustering analysis was largely consistent with the PCoA, supporting the existence of three groupings of islands (Figure 5b). In contrast, the PERMANOVA test failed to show significant differences in the floristic composition of invasive species among these island groups (pseudo- $F_{1,6} = 1.488$ ,  $p$ -value > 0.05).

**TABLE 1** Fixed effect optimization rank of the generalized mixed models performed for species richness of invasive alien plants in the Canary Islands. df, degrees of freedom; Log (L), maximized log-likelihood; the AICc, AICc difference ( $\Delta$ AICc); and Akaike weights derived from the AICc ( $AICc_w$ ) are given for each model. The proportion of the total variation in species richness among islands ( $R^2$ ) that is accounted for by selected GLMMs is indicated

	df	log (L)	AICc	$\Delta$ AICc	$AICc_w$	$R^2$	
						Conditional	Marginal
Species Richness ~ Intercept + Origin + (1 Island)	12	-123.2	276.0	0.0	1	0.83	0.77
Species Richness ~ Intercept + (1 Island)	2	-323.2	650.6	374.6	0.0	0.24	0

### 3.5 | Which factor best explains invasion within the archipelago?

The GDM results showed that the full model that includes the three environmental variables (diurnal temperature range, temperature seasonality and precipitation seasonality), pairwise geographic distances and pairwise distances by human transportation explained 68.5% of the deviance. When the significance of the model and the importance of the variables were assessed, we found that only two variables have a significant contribution to the model ( $p$ -value < 0.05; Figure 6): precipitation seasonality (sum of l-spline coefficients = 0.5) and geographic distance (0.27). The final model, including these two variables as predictors, explained 67.96% of the deviance and was statistically highly significant ( $p$ -value < 0.001).

## 4 | DISCUSSION

We showed that the Neotropical region is the main source of plant invasions to the Canary Islands, outnumbering those from other regions with a general Mediterranean-type biogeographic region. Our results thus provide additional evidence that floristically distant regions can become important sources of harmful invaders (Daehler, 2003; Fridley, 2008; Seastedt & Pyšek, 2011), arguing for alternative context-dependent explanations for the underlying mechanisms that might contribute to invasion success on islands. Although we observed a slow increase in numbers of invasive species until the 1950s, followed by a stronger rise subsequently, we failed to detect significant differences in naturalization rates among groupings defined by their biogeographic origins. In order to explain composition dissimilarity of the invasive flora among islands, a climatic similarity hypothesis was fully supported, with geographic isolation and human-mediated connectivity hypotheses receiving less and null support respectively. The assembly of the invasive plant flora within the archipelago thus appears to be driven primarily by climate, but with geographic distance also playing a role.

### 4.1 | Biogeographic origins of an invasive alien island flora

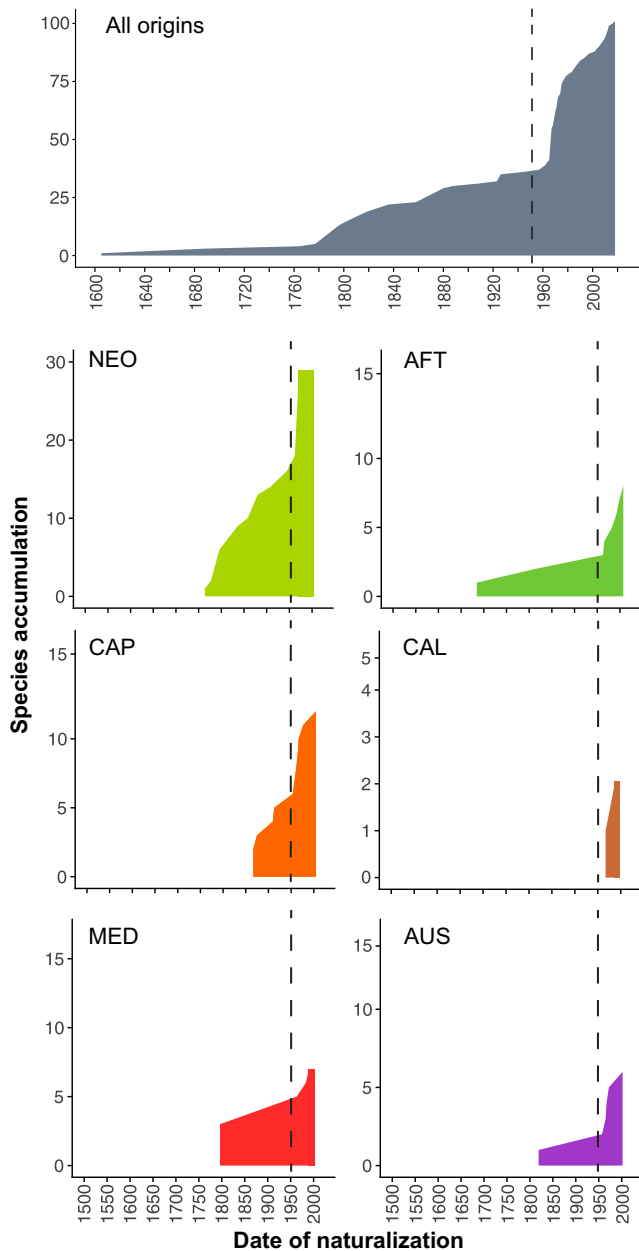
Based on a floristic-driven approach, we showed that vascular plant introductions from Neotropical regions to the Canary Islands

outnumbered those from other regions with a similar Mediterranean-type bioclimate. Indeed, the most diverse alien genera (e.g. *Agave*, *Opuntia* and *Cylindropuntia*) were of Neotropical origin. Our results are thus at odds with the often-invoked 'Imperialist Dogma' (sensu Di Castri et al., 1990) and previous findings supporting that plant introductions are predominant from Europe to elsewhere (Monnet et al., 2020; Seebens et al., 2017; van Kleunen et al., 2015), and from the Iberian Peninsula to other Mediterranean-type regions or vice versa (Cao Pinna et al., 2021; Casado et al., 2018; Di Castri et al., 1990; Fox, 1990). In doing so, we rejected our first hypothesis and provided novel evidence for the importance of the historical socio-economic factors when explaining the underlying mechanisms of plant invasion (Chapman et al., 2017; Seebens et al., 2015).

The present study is not the first that would appear to lead to rejection of the climate matching hypothesis between source and sink regions of invasive alien plants. The historical exchange of goods (Jaksic & Castro, 2021) and a disproportionate representation of plants with economic value (van Kleunen et al., 2020) have been indeed suggested as more important drivers explaining the overrepresentation of European taxa elsewhere rather than actual biological pre-adaptation. However, the archipelago of the Canary Islands is an environmentally complex territory, which exhibits important climatic variations in longitude and elevation (del Arco-Aguilar & Rodríguez-Delgado, 2018). For instance, the level of precipitation ranges from hyperarid to humid, depending on the island, with the coastlands exhibiting lower levels of precipitation (i.e. 50–500 mm) compared with northern slopes (800–1300 mm; del Arco-Aguilar & Rodríguez-Delgado, 2018). Hence, our study provides support for the role of a non-Mediterranean biogeographic region as a main source of invasive species to the archipelago rather than evidence for the acceptance or the rejection of the climate matching hypothesis. Three potential limitations of the present study can explain this lack of resolution.

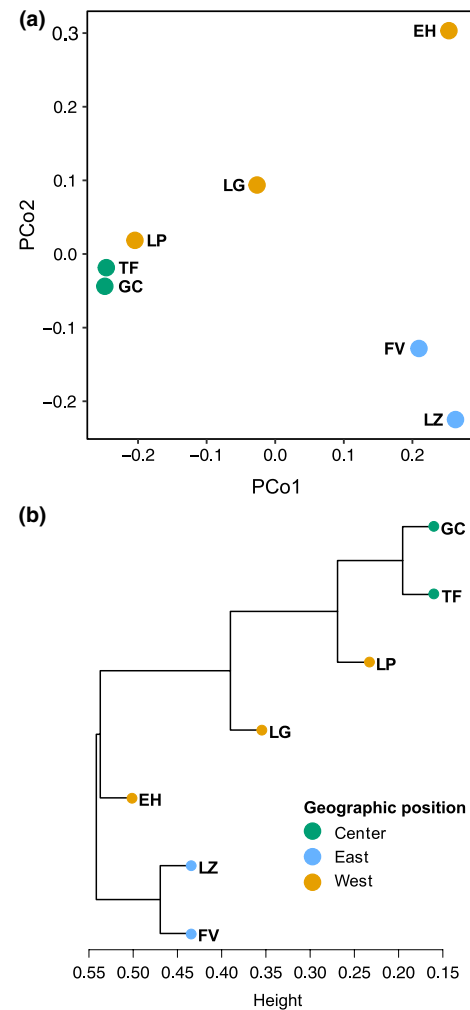
A first drawback would be related to the fact that the Neotropics is home to more than twice as many plant species as, for instance, the Cape Region and tropical Africa together, or as tropical Asia alone (Raven et al., 2020). Although our study does not account for these differences in species richness across all the source regions, recent evidence supports the crucial role of transport and trade networks as well as human disturbance in explaining global patterns of emerging alien species (Seebens et al., 2018). Second, we used a coarse spatial-grained biogeographic classification to explore source-sink relationships of an invasive alien flora in an oceanic archipelago.





**FIGURE 4** Temporal patterns in first record rates of naturalization represented by accumulation curve areas of invasive alien plant species. For visualization, 20-year and 50-year periods are distinguished for all origins and each biogeographical region respectively. Time series for biogeographic regions with low numbers of first records are not shown. NEO, Neotropics; AFT, Tropical Africa; CAP, Cape Region of South Africa; MED, Mediterranean Basin including Europe, North Africa and Middle East; AUS, Australasia; CAL, California. The dashed line denotes the beginning of the 1950s.

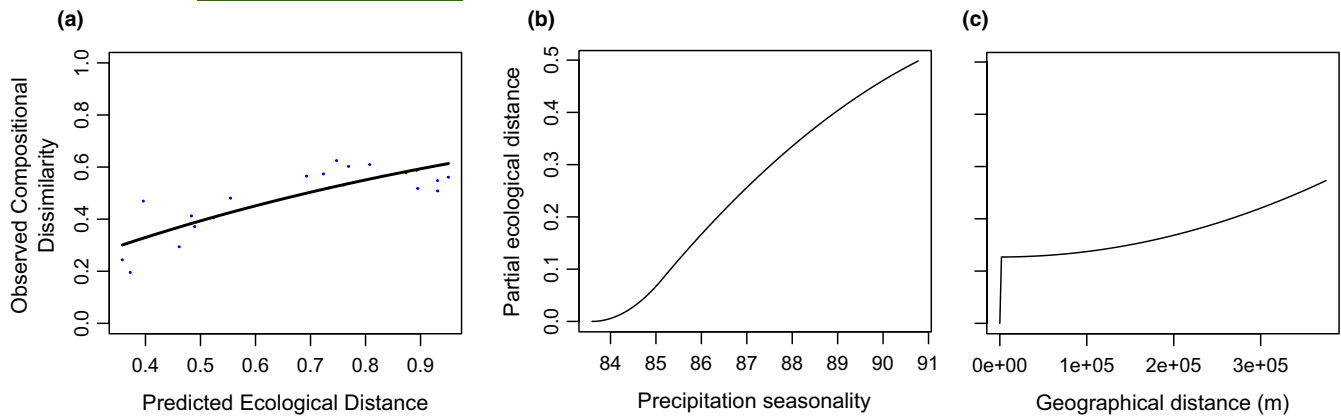
Lastly, the main transport hubs are located in the low, dry, warm south-eastern areas in each of the Canary islands, which might have increased the introduction risk of species with such ecological requirements. Our approach, therefore, renders the question of the extent to which climate matches between the main species source pools and the Canary archipelago open.



**FIGURE 5** Clustering of the seven main Canary Islands according to their differences in invasive alien plant species assemblages. General biogeographical patterns inferred from: (a) principal coordinate ordination (PCoA) analysis and (b) hierarchical classification using weighted arithmetic average clustering (WPGMA) as the linkage method. Acronyms in each plot represent each island as follows: LZ, Lanzarote; FV, Fuerteventura; GC, Gran Canaria; TF, Tenerife; LG, La Gomera; LP, La Palma; EH, El Hierro.

## 4.2 | The tempo of invasion

It has previously been proposed that introductions peaked during the last 200 years due to (i) major migration waves of European settlers in the 18th and 19th century and (ii) the acceleration of global trade in the 20th century, with Europeans bringing most species they liked or needed from home (Hulme, 2009; Seebens et al., 2015; Seebens et al., 2017). Accordingly, our study demonstrates that most of the floristic groupings considered, including the Mediterranean Basin, did not show any sign of saturation, rather their rates of naturalization increased during the 1950s or thereafter. Moreover, the magnitude of the increase in the number of invasive alien species varies considerably among biogeographic regions, with a different balance of source regions in recent times compared to historical



**FIGURE 6** Generalized dissimilarity modelling (GDM) results. (a) Relationship between the observed pairwise floristic dissimilarity in invasive alien species between islands and the ecological distance predicted by the preferred GDM model (predicted ecological distance between islands). (b–c) GDM-fitted I-splines for each predictor of the preferred model: Precipitation seasonality and geographic distance. The sum of coefficients of the fitted I-splines (maximum height of the curve) indicates the predictor importance in explaining the floristic composition dissimilarity of invasive alien species.

times. All these findings lead to the support of the *Naturalization Rate Hypothesis* (H2).

Based on our results, we propose that the incidence of naturalizations of Mediterranean (and European) plants in the Canary archipelago during the historical European human diaspora was insignificant. Since the first colonial European voyages, through to the present, commercial routes from Europe were established as bidirectional, transiting through the Canary Islands for connections with central and South America and tropical Africa (Aldrich & Connell, 1998; Armenteros Martínez, 2018; Bosa, 2004; Parsons, 1983; Santana-Pérez, 2018). This historical dynamic provides support for two non-exclusive potential explanations.

The first explanation implicates the Canary and European migrant groups that have travelled back to the Canary Islands during different waves from regions such as Mexico, Cuba, Venezuela and Uruguay (Parsons, 1983), particularly under flourishing socio-political periods in the archipelago. From where, and how many of these returned remain open questions (James, 1985). In addition, the Canary archipelago has played a historical role as a hub for European–American trading routes, with trade connectivity increasing over time (Aldrich & Connell, 1998; Bosa, 2004; Parsons, 1983). These migration and trade circumstances have produced concentrated migration that likely explains the high rates of invasion by alien plant species from Central and South America, mainly for agricultural and horticultural purposes (e.g. González, 2008; Verloove et al., 2019). All these historical changes in networks of human migration and commerce from and to the Canary archipelago exemplify the need for revisiting the original ‘Imperialist Dogma’ hypothesis (Crosby, 2004; Di Castri, 1989; Di Castri et al., 1990), in order to accommodate the emerging patterns and challenges arising from accelerating rates of global change associated with increasing human trade and transport.

With regard to the second explanation, it may be possible that additional alien species of Mediterranean Basin origin have been incorrectly considered as native, due to an apparent limited

geographic and environmental distance between these continental and insular regions. This could significantly reduce the number of species categorized as ‘invasive’ or ‘naturalized’ and inflate the number of species wrongly considered as ‘probably native’ included in the regional species checklist BIOTA (<https://www.biodiversidadcanarias.es/>). This potential source of uncertainty calls for genetic approaches to identify and confirm the alien status of cryptogenic plant species (Brandes et al., 2019; Briski et al., 2016), namely if they exhibit efficient dispersal capabilities (Patiño & Vanderpoorten, 2015).

### 4.3 | Within-archipelago assembly mechanisms

Our analyses show that the floristic composition of invasive plants is strongly determined by climatic similarity within the archipelago and, to some extent, by geographic distance. This result is puzzling because of the signature of floristic homogenization evidenced by the fact that: (i) the different floristic elements exhibited consistent proportions across the Canary Islands; (ii) most invasive alien species occur in several islands; and (iii) PERMANOVA tests were not significant. However, consistent with the *Within-archipelago Climate Matching Hypothesis* (H3), Lanzarote and Fuerteventura are floristically more similar, which can be explained by the fact that these two islands are the driest, topographically simplest and geographically nearest (del Arco-Aguilar & Rodríguez-Delgado, 2018). Indeed, the arrangement and apparent groupings of the islands along the second PCoA axis reveal a pattern that could be explained, to some extent, by differences in precipitation, topography and longitude (del Arco-Aguilar & Rodríguez-Delgado, 2018). Overall, there is indeed congruence between the inter-island composition differences in invasive floras identified here and the classic floristic delineation inferred from Canary native assemblages (de Nicolás et al., 1989). The latter has often identified two floristic entities, Lanzarote-Fuerteventura versus central and western

islands (del Arco-Aguilar & Rodríguez-Delgado, 2018). Therefore, our data imply that climate similarity and geographic distance can interact (i.e. closer islands have a more similar climate than more distant islands) to shape assemblages of invasive plants on islands. Such an observation is in line with former evidence for other floristic and geographic contexts (e.g. Cao Pinna et al., 2021; Capinha et al., 2015; Monnet et al., 2020).

However, our proxies for environmental distance are based on temperature and precipitation at the scale of 1-km<sup>2</sup> cells (Fick & Hijmans, 2017) that can be poor descriptors of actual climatic gradients in topographically complex small islands (e.g. Ferreira et al., 2016). In addition, climate similarity has been shown to be less evident on subtropical, high-elevation islands, which often exhibit a broad array of climate zones due their high topographic complexity (Essl et al., 2019; Kueffer et al., 2010). Although such distributional patterns on islands and their underlying mechanisms need further research (Lenzner et al., 2020; Patiño et al., 2017), we expect that climatic similarity would gain importance versus geographic isolation, if finer spatial-scale species distribution and climate data can be considered in future studies.

Our statistical approach provided no support for a pattern of human-mediated connectivity mechanisms. This result is at odds with our *Enhanced Connectivity Hypothesis* (H4) and former evidence supporting the role of trade networks (Chapman et al., 2017; Hulme, 2009; Seebens et al., 2015). Such a finding is likely the combined result of different factors. First, the available transport network datasets cover a short period of time (i.e. less than 20 years), while most introduction and naturalization episodes have happened earlier (76%; see Appendix S1). Second, as demonstrated for other regions and taxonomic groups (Chapman et al., 2017), we expect that the live plant trade in the Canary Islands might have significantly contributed to explain recent introduction episodes of invasive plants to and across the Canarian archipelago. This is remarkable at the regional scale because the journeys between islands experienced by alien live plants and their propagule are short, which ultimately facilitates invasion success driven by live plant imports (Seebens et al., 2015; van Kleunen et al., 2018). Despite the high uncertainty in the directionality and intensity of historical trade networks (Cao Pinna et al., 2021), recent trade networks (i.e. after the 1950s) might explain invasion success due to the increasing volumes handled by sailing container shipping and commercial jet aviation, and the rise of the international e-commerce (Hulme, 2021). Thus, to what extent invasions driven by live plant trade have taken place among already invaded or native-invaded ecological systems remains largely untested in many regions, like the Canary Islands.

## 5 | CONCLUSIONS

We provide evidence that biogeographic affinities are not always the most important factors determining the predominant

continental sources of alien plant species to insular recipients, even if they differ in their invasiveness status (i.e. invasive vs. naturalized). Both climate similarity and geographic distance are clearly important in explaining floristic relationships of the invasive flora within the Canarian archipelago. Nevertheless, our results also illustrate how archipelago-dependent processes can cause idiosyncratic, yet prevalent patterns of invasion success, ultimately reinforcing the view of biotic homogenization as a main driver of insular floras (Castro et al., 2010; Kueffer et al., 2010; Sánchez-Ortiz et al., 2020).

From a more applied perspective, our study helps to understand the biogeographic origins of the invasive alien flora of the Canary Islands, highlighting the need to control and monitor alien species of non-Mediterranean origin. Among these taxa, we find many examples within the most biodiverse Neotropical group (e.g. *Opuntia* spp., *Agave* spp., *Cylindropuntia* spp., *Austrocylindropuntia* spp., *Furcraea foetida*, *Prosopis juliflora*), which are predominantly composed of species with ecological affinity for arid habitats such as deserts or savannahs (Eguarte et al., 2021; Filip et al., 2017; Guerrero et al., 2019). In this respect, these species often occur in disturbed lowlands (e.g. cliffs next to sea; Filip et al., 2017; Haider et al., 2010) and anthropogenic corridors (e.g. roadsides; Arévalo et al., 2005; Bacaro et al., 2015; Irl et al., 2021) across arid areas in the archipelago. The heavily human-disturbed lowlands and coastlands, including arid and semiarid coastal scrubs and semiarid thermophilous woodlands (del Arco-Aguilar & Rodríguez-Delgado, 2018), are therefore more likely to be invaded by new arrivals from within this biogeographical grouping, particularly under ongoing climate change. A similar pattern has been proposed for continental Spain (Andreu & Vilà, 2010), which might be particularly aggravated by global warming. Effective biosecurity policies to regulate ornamental trade, especially those promoted by xero-gardening, and importations from Neotropics and arid regions should become a management priority in the Canarian and, most probably, Macaronesian regions. This conclusion urgently calls for the cooperation of the horticultural and tourism industries.

## ACKNOWLEDGEMENTS

This research was supported by the Fundación BBVA project (INVASION - PR19\_ECO\_0046) and the Spanish Ministry of Science and Innovation (MICINN) project (ASTERALIEN - PID2019-110538GA-I00). J.M.-L. was funded by the INVASION Fundación BBVA project and by a Juan de la Cierva-Formación Fellowship (MICIIN; reference FJC2020-046353-I). Y.A. by the ASTERALIEN MICINN project. J.P. was funded by the MICINN through the Ramón y Cajal Program (RYC-2016-20506). L.S.J.G. was funded by the Academia Canaria de Investigación Gobierno de Canarias FPI 2021 Fellowship (TESIS2021010101). The authors also thank Dr. D. Chapman and two anonymous reviewers for their constructive comments and suggestions. No permits were needed to perform this study.

## CONFLICT OF INTEREST

The authors declare that we have no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this research can be found in the Supporting Information.

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### BIOSKETCH

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**Author contributions:** Jairo Patiño and Marcos Salas-Pascual conceived the idea and designed the study. Marcos Salas-Pascual, J. Alfredo Reyes-Betancort, Antonio García-Gallo and Jairo Patiño assembled the data. Agustín Naranjo-Cigala prepared the cartography. Javier Morente-López, Yurena Arjona and Louis S. Jay-García carried out all statistical analyses. JP wrote the first draft of the manuscript. All co-authors contributed substantially to revisions. Editor: Daniel Chapman.

### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Morente-López, J., Arjona, Y., Salas-Pascual, M., Reyes-Betancort, J. A., del Arco-Aguilar, M. J., Emerson, B. C., García-Gallo, A., Jay-García, L. S., Naranjo-Cigala, A., & Patiño, J. (2023). Biogeographic origins and drivers of alien plant invasions in the Canary Islands. *Journal of Biogeography*, 00, 1–15. <https://doi.org/10.1111/jbi.14556>