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Research Article

Moving beyond environmental filtering hypotheses: Deciphering the drivers of congeneric plant introductions in an oceanic archipelago

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Understanding why only some species succeed in naturalizing and invading ecosystems has intrigued scientists since Darwin's time. The pre-adaptation hypothesis posits that introduced species closely related to natives, therefore ecologically similar, are more likely to establish than others. This aligns with the climate matching hypothesis, by which mismatches between species' ecological requirements and local conditions act as barriers to establishment and naturalization. Conflicting evidence leaves the respective roles of biogeographic origin and climatic affinity in invasion risk prediction unresolved. Here, we examine how biogeographical origin, climatic matching, and phylogenetic relatedness influence the success of introduced plant species that are congeneric with native species in the Canary Islands, an oceanic archipelago with Mediterranean climatic affinities. We integrated phylogenetic, climatic and occurrence data at two levels: 1) interspecific comparisons of phylogenetic distances and climatic overlap between introduced species and their closest native counterpart; and 2) intra-specific analysis of realized climatic niches between native and invaded ranges. Most congeneric species originate from the Mediterranean Basin and temperate Europe and, to a lesser extent, the Neotropics. Phylogenetic distance did not significantly contribute to climatic overlap between native and introduced congeneric species, ruling out the pre-adaptation hypothesis and questioning the generality of phylogenetic niche conservatism in promoting invasion success. Intraspecific analyses showed that over one-third of species exhibited an expansion of their realized climatic niche towards climatic space not occupied in the native ranges. These results indicate that climatic niche expansion, potentially driven by ecological release from natural or anthropogenic biotic constraints, or by in situ evolution, may represent an important process in biological invasions. Our findings highlight the prevalence of niche expansion among

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introduced plant species in the Canarian archipelago and suggest a role in facilitating invasion within this archipelagic context, with potential implications for risk assessment in increasingly disturbed insular regions worldwide.

Keywords: biogeographic regions, biological invasions, Canary Islands, climate matching, phylogenetic relatedness, realized climatic niche

Introduction

Biological invasions are major drivers of global change, posing significant threats to human health, economies, and biodiversity (Cronk and Fuller 2014, Py  sek et al. 2020), with their most severe consequences being the extinction of native species (Bellard et al. 2016, Orihuela-Rivero et al. 2025). Anthropogenic introductions have also accelerated the global loss of taxonomic uniqueness, resulting in the biotic homogenization of both floras and faunas (Seebens et al. 2017, Daru et al. 2021, Yang et al. 2021). This trend of increasing species naturalization and uniqueness loss is projected to intensify in the coming decades (van Kleunen et al. 2015, Hulme 2021), underscoring the urgent need to investigate the ecological and evolutionary shifts of introduced species within invaded ranges as well as their interactions with native biotas.

To better understand the mechanisms driving biological invasions, a range of hypotheses and frameworks have emerged from empirical studies (Blackburn et al. 2011, Dai et al. 2020, Gioria et al. 2023). Among these, Charles Darwin (1859) addressed the issue of biological invasions in his seminal book ‘On the origin of species’. Darwin’s ‘pre-adaptation hypothesis’ (hereafter DPAH; Duncan and Williams 2002) suggests that evolutionary relatedness can provide an advantage through shared pre-adaptations to similar environmental conditions (Thuiller et al. 2010). In practice, phylogenetically related introduced species may have a higher likelihood of establishment due to their evolutionary and ecological similarities with native species (Park and Potter 2013, Cadotte et al. 2018). Such a premise emphasizes the importance of phylogenetic niche conservatism in biological invasions (Broennimann et al. 2012, Petitpierre et al. 2012, Guisan et al. 2014). Evidence both supporting and challenging the DPAH has been derived from a wide range of studies, including taxonomic, trait-based, and phylogenetic analyses, as well as experimental approaches (Daehler 2001, Cadotte et al. 2009, 2018, Park and Potter 2013, 2015, Marx et al. 2016). Climate-based approaches, however, have received comparatively less attention in the literature (Cadotte et al. 2018).

Nested within DPAH, the ‘climate matching hypothesis’ (CMH) is one of the most widely recognized frameworks for understanding the exchange of introduced species across biogeographic regions. The CMH suggests that introduced species are more likely to establish in areas where climatic conditions resemble those of their native range (Thuiller et al. 2005, Richardson and Thuiller 2007, Broennimann et al. 2021). Rooted in the concept of environmental filtering,

CMH suggests that mismatches between a species’ ecological requirements and local conditions act as barriers to establishment and naturalization (Richardson and Py  sek 2012, Enders et al. 2020). Accordingly, CMH assumes that introduced species succeed when they encounter environments analogous to those they are evolutionarily (pre-)adapted to (Guisan et al. 2012); an idea sometimes linked to the notion of ‘pre-adaptation’. However, to avoid confusion with DPAH, we refrain from using that definition here. Recent conceptual and analytical advances in niche theory provide a valuable framework to assess whether introduced species remain constrained within their native realized climatic niches (i.e. the portion of the fundamental niche shaped by competitive interactions and other limiting factors, sensu Hutchinson 1957, but see also Pearman et al. 2008). This perspective enables testing of intraspecific niche conservatism and its role in structuring biological invasions (Broennimann et al. 2012, Early and Sax 2014).

Empirical support for CMH is controversial (Guisan et al. 2014). Some studies suggest that introduced plant species typically thrive in climates that closely resemble those of their native ranges, showing limited climatic niche shifts (Petitpierre et al. 2012, Liu et al. 2020). Conversely, substantial evidence also points to niche shifts, whereby species occupy climatic conditions in the invaded range that do not overlap with the native realized niche (Hill et al. 2017, Atwater et al. 2018). Indeed, a recent review found that ca. 65% of studies reported evidence of niche shifts during biological invasion (Bates and Bertelsmeier 2021). The latter, however, suggest this apparent prevalence may partly result from publication bias, as studies confirming niche conservatism may be underreported. Understanding the interplay between CMH and DPAH is crucial, as climate is a major driver of floristic patterns globally (van Kleunen et al. 2015, Mucina 2019, Enders et al. 2020, Irl et al. 2021, Yang et al. 2021). This is particularly important for assessing the extent to which introduced species can adapt to novel climatic conditions, potentially revealing their capacity for ecological niche shifts (Early and Sax 2014).

Oceanic island floras rank among the most vulnerable ecological systems to biological invasions (Donlan et al. 2003, Sax and Gaines 2008, Py  sek et al. 2012, Carine and Sequeira 2020). Their susceptibility to human-mediated naturalization stems not only from their disharmonic species pools (K  nig et al. 2021), but mostly from the evolutionary outcomes of volcanic origin and long-term isolation (Whittaker et al. 2023). As a result, insular biotas often exhibit key innovations, collectively referred to as insular syndromes (Adler and Levins 1994), such as body size shifts

(Lomolino et al. 2013), altered dispersal ability (Carlquist 1974, Burns 2019), insular woodiness (Lens et al. 2013), and reduced defences against herbivores (Carlquist 1974, Burns 2019). While these traits are adaptive in pristine island environments, they also contribute to making insular communities particularly vulnerable to human-mediated disturbance and biological invasions (Simberloff 1995, Caujap  -Castells et al. 2010, Dawson et al. 2017, Lenzner et al. 2020), although their causal mechanisms and ecological consequences remain debated (Burns 2019).

In the present study, we focus on the flora of the Canary Islands. Using an integrative approach based on climatic envelopes (i.e. the climatic component of the ecological niche or the 'realized climatic niche', Pearson and Dawson 2003), we compiled biogeographic, phylogenetic, and occurrence data for both native and introduced plant species. We then tested the DPAH through interspecific comparisons, and the CMH through intraspecific comparisons within a two-step

framework (Fig. 1). To minimize potential biases associated with predominant biogeographic affinities in the introduced flora (Morente-L  pez et al. 2023), interspecific analyses were restricted to extant genera containing both native and introduced species (Steen et al. 2024). Focusing on congeneric pairs of native and introduced species, which often share functional traits and evolutionary histories (Yin et al. 2021, Steen et al. 2024), provides a robust framework for identifying features associated with invasiveness or resistance to invasion (Daehler 2001, Strauss et al. 2006, Steen et al. 2024). In a second step (Fig. 1), we assessed the importance of climatic niche shifts through intraspecific analyses of introduced taxa between their native and invaded ranges.

Specifically, we address the following questions: 1) which climate types and biogeographic regions are associated with the presence of congeneric native and introduced plant species within the Canaries? 2) Is phylogenetic relatedness linked to climatic overlap between native and introduced congeners,

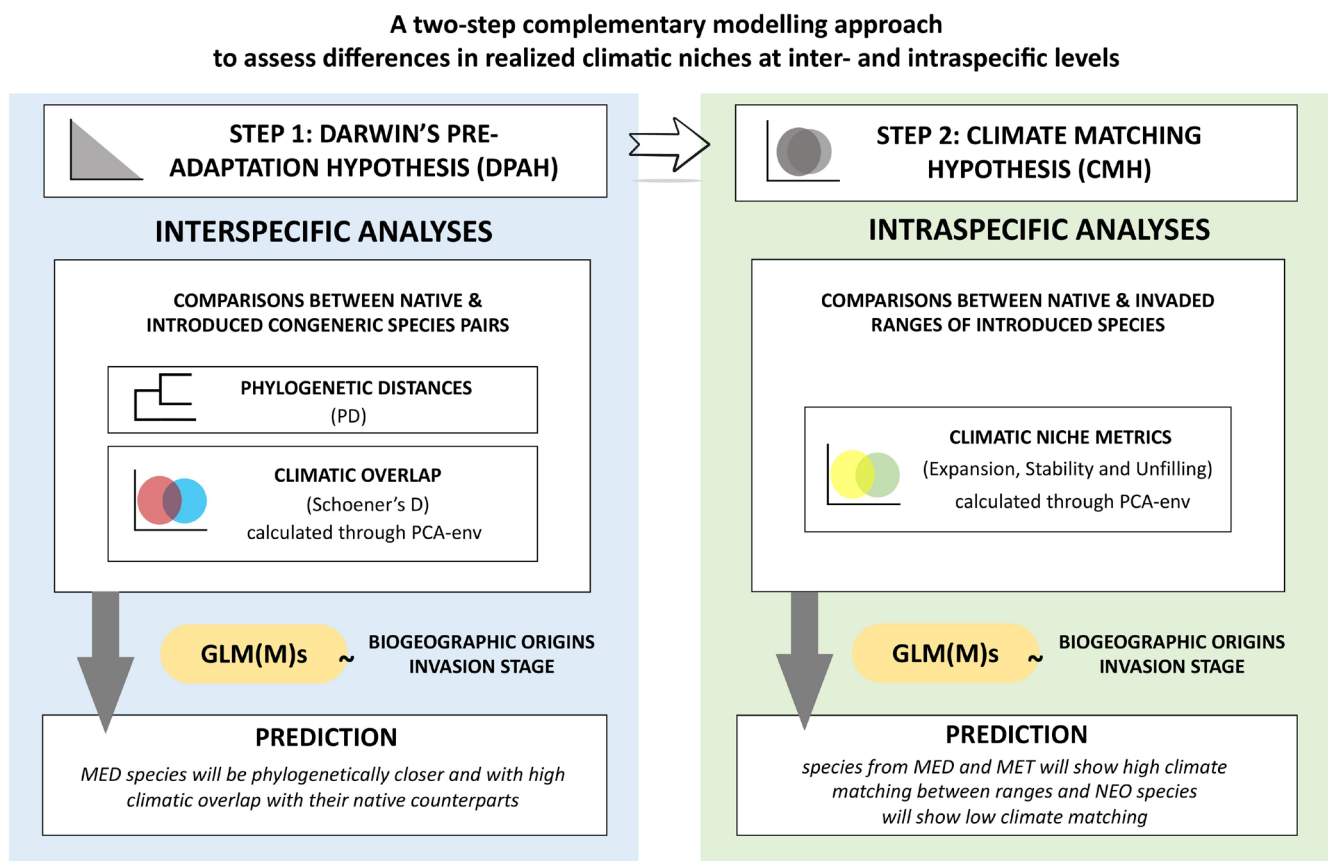


Figure 1. Methodological framework summarizing the two-step analytical workflow used to evaluate the roles of biogeography, climate, and phylogeny in realized climatic niche patterns of the introduced flora in the Canary Islands. Left panel (interspecific analyses testing 'Darwin's pre-adaptation hypothesis', DPAH): comparisons between each introduced species and its closest native congeneric species, quantifying phylogenetic distance (PD) and climatic niche overlap (Schoener's *D* derived from PCA-env). These metrics are analyzed in relation to biogeographic origin and invasion stage using GLM(M)s to evaluate predictions of DPAH. Right panel (intraspecific analyses testing the 'climate matching hypothesis', CMH): comparisons between native and invaded ranges of introduced species, estimating realized climatic niche metrics (expansion, stability, and unfilling) within PCA-env space. Resulting metrics are related to biogeographic origin and invasion stage using GLM(M)s to test expectations of the CMH. MED, Mediterranean Basin; MET, other Mediterranean-type regions (Cape Floristic Region, California Floristic Province, central Chile, southwestern Australia); NEO, Neotropics.

consistent with interspecific phylogenetic niche conservatism as a driver of invasion success? 3) To what extent do realized climate niches differ between native and invaded ranges, while accounting for species' biogeographic origin? Building on evidence that biodiversity hotspots with Mediterranean-type climates disproportionately receive introductions from climatically similar regions (Casado et al. 2018, Cao Pinna et al. 2021), we hypothesize that closely related introduced species mostly originate from the Mediterranean Basin and exhibit high climatic niche overlap with both their native congeners and native ranges, reflecting strong inter- and intraspecific niche conservatism.

Material and methods

Study area

The Canary Islands, an oceanic archipelago located in the northeast Atlantic Ocean, belong to the Macaronesian biogeographic region (Fig. 2A; Fernández-Palacios et al. 2024). The archipelago is characterized by a subtropical Mediterranean climate, with mild temperatures and seasonally variable precipitation shaped by trade winds, oceanic influence, and complex topography (del Arco-Aguilar and Rodríguez-Delgado 2018). A persistent thermal inversion limits vertical cloud development, producing the characteristic 'sea of clouds', which supplies moisture to zonal ecosystems such as the laurel forests via horizontal precipitation, while lowland areas remain arid (del Arco-Aguilar and Rodríguez-Delgado 2018, Patiño et al. 2023).

The archipelago is a well-established model for studying biodiversity patterns and underlying ecological and evolutionary processes (Florentio et al. 2021). It represents a westward extension of the Mediterranean Basin Hotspot into the Atlantic (Médail and Quézel 1997), and is noted for exceptional endemism, with ~ 40% of the native vascular flora being endemic (del Arco-Aguilar and Rodríguez-Delgado 2018). The region also harbours around 900 introduced species, accounting for ca 32% of the total flora (Gobierno de Canarias 2025). Our study focuses on seed plant genera containing both native and introduced species, comprising 97 genera and 631 congeneric species, representing 30% of the introduced flora and 22% of the native flora (Gobierno de Canarias 2025).

The Canary Islands provide a particularly informative case study for biological invasions. Although both the climate and native flora are predominantly Mediterranean in origin (Carine et al. 2010, del Arco-Aguilar and Rodríguez-Delgado 2018), the dominant biogeographic origin of invasive introduced plants is the Neotropics, exceeding contributions from other Mediterranean-type regions (Morente-López et al. 2023). This pattern likely reflects a combination of high Neotropical species richness (Raven et al. 2020); historical trade and migration links with the Americas (Parsons 1983); the rarity of snowfall and freezing temperatures, particularly below 1800 m a.s.l. (del Arco-Aguilar and Rodríguez-Delgado 2018); and the potential misclassification of long-established

introductions as native species, particularly of those with a Mediterranean origin (Morente-López et al. 2023). While this assemblage may initially appear to challenge both the CMH and DPAH, explicit analyses of the realized climatic niches occupied by introduced species in the archipelago are essential to critically evaluate these hypotheses.

Origin and biogeographical classifications

Each species was assigned native or introduced status based on the Biodiversity Data Bank of the Canary Islands (hereafter BIOTA, Gobierno de Canarias 2025). Following the framework of invasion as a continuum (Richardson et al. 2000, Blackburn et al. 2011), we focused on the naturalization and invasion stages. Accordingly, introduced species are hereafter categorized as either naturalized or invasive when referring to the invasion stage (Richardson et al. 2000).

To determine the native ranges of introduced species that are congeneric to native species in the Canary Islands (hereafter, congeneric species), we retrieved distribution data of their native geographic areas or 'botanical countries' as described by the World Geographical Scheme for Recording Plant Distributions (Brummitt 2001). Climate affiliations of each species were extracted from the World Checklist of Vascular Plants (Govaerts et al. 2021), which categorizes species into broad climate zones: temperate, subtropical, seasonally dry tropical, wet tropical, and desert and dry shrubland. This database was supplemented using Plants of the World Online (POWO, accessed between September 2022 and June 2023).

Furthermore, species were assigned to one or more native biogeographical regions following Morente-López et al. (2023). These regions include: the five Mediterranean-type climate regions (Mediterranean Basin, Cape Floristic Region, California Floristic Province, central Chile, and southwestern Australia); Palearctic Europe excluding the Mediterranean Basin, hereafter temperate Europe; Nearctic or temperate North America excluding the Californian Province; Neotropics or tropical America excluding central Chile; tropical Africa excluding the Maghreb, Sahara, and Cape Region; Palearctic East Asia; tropical Asia; Australasia; and cold or hot (semi)deserts (Brummitt 2001). Species present in more than one region were further reviewed using additional literature sources to determine the most appropriate classification (Supporting information). Those with broad, disjunct, or cosmopolitan distributions were classified as widespread (Morente-López et al. 2023). Species presence across regions was recorded in a presence-absence matrix (Fig. 1). For statistical analyses, we finally focused on the most represented regions with sufficient sample size: the Mediterranean Basin, the other Mediterranean-type climates (i.e. Cape Floristic Region, California Floristic Province, central Chile, and southwestern Australia), temperate Europe, and the Neotropical regions.

Occurrence data

Out of the 97 genera containing both native and introduced congeneric species, 15 were excluded due to insufficient occurrence data for their native range (i.e. fewer than 10

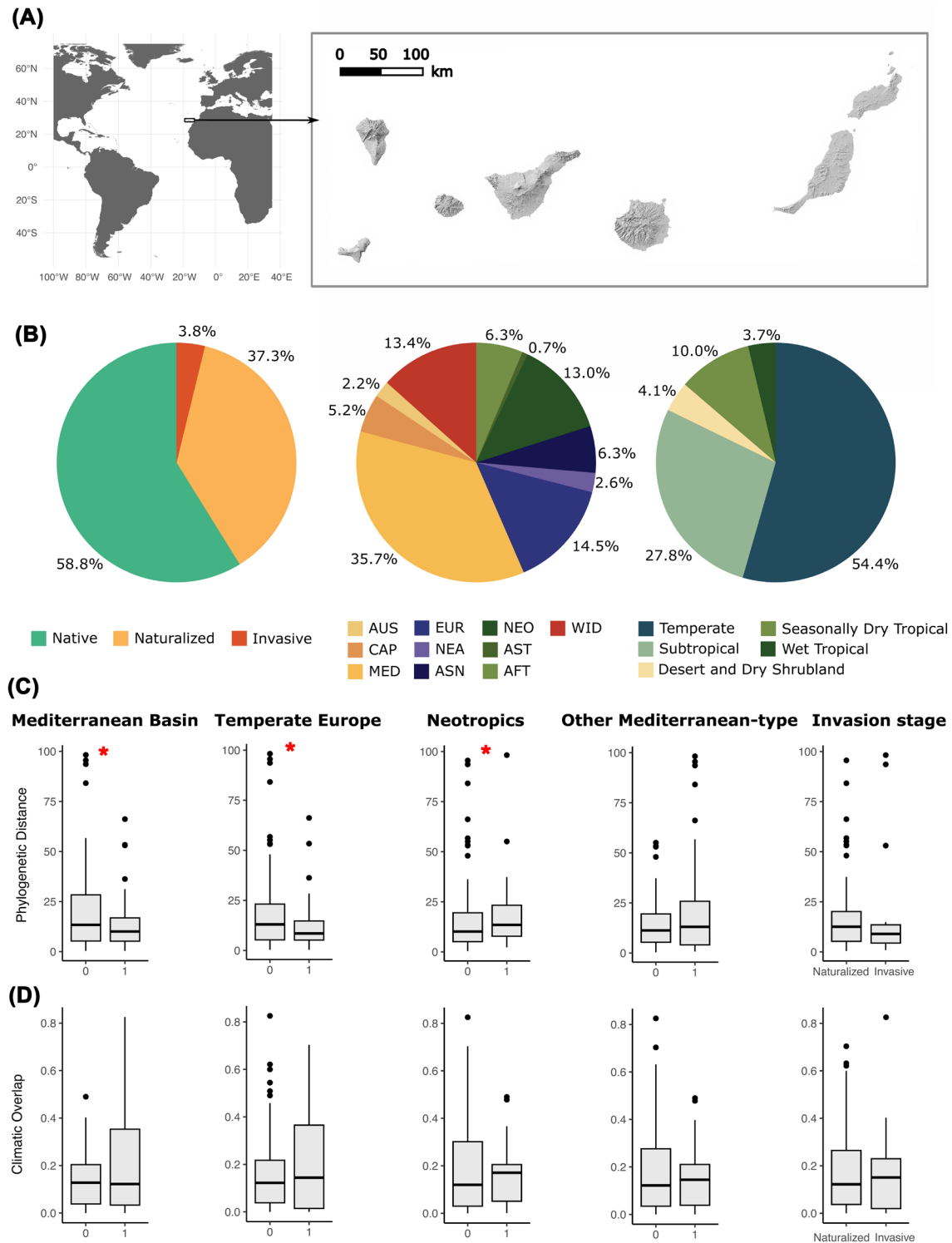


Figure 2. (A) Geographic location of the study area (Canary Islands) in a global context. (B) Proportions of introduced congeneric species in the Canary Islands ($n=268$) according to their invasion stage, primary biogeographic region of native origin, and predominant climatic zone following Govaerts et al. (2021). (C)–(D) Boxplots showing phylogenetic distance (C) and climatic overlap with the closest native congener (D) for analyzed species pairs ($n=182$), grouped by native presence (1) or absence (0) in each major biogeographic region (Mediterranean Basin, temperate Europe, the Neotropics and other Mediterranean-type climates) and by invasion stage (naturalized versus invasive). Asterisks (*) indicate statistical significance ($p < 0.05$). Australasia (AUS); Cape Floristic Region (CAP); Mediterranean Basin (MED); Temperate Europe excluding the Mediterranean Basin (EUR); Temperate North America (NEA); Southwestern Australia (ASN); Tropical America excluding central Chile (NEO); tropical Asia (AST); tropical Africa excluding the Maghreb, Sahara, and Cape Region (AFT); Widespread (WID).

occurrences for some or all species of a given genus with presence in the archipelago) or because neither native nor introduced species were represented in our backbone phylogeny (Supporting information). The remaining 82 genera (84.5% of the total) were retained for interspecific analyses (Step 1 in Fig. 1), encompassing 182 introduced species (67.4% of all introduced congeneric species; Supporting information) and 405 native species.

For intraspecific comparisons between native and invaded ranges (Step 2 in Fig. 1), an additional 62 species were removed due to insufficient occurrence data in the invaded range. Consequently, the following analyses were based on data for 65 genera with a specific number of 120 introduced species (44.6% of all introduced congeneric species; Supporting information).

We gathered species occurrence data from 1970 to the present. For the Canary Islands, distribution data were retrieved from the BIOTA platform (Gobierno de Canarias 2023). For the native ranges of introduced species and the non-Canarian ranges of native species, we used GBIF (GBIF 2023). Concerning data in the BIOTA database, we only retrieved records at the first two levels of resolution, using centroids of each 500 × 500 m grid cell. Raw GBIF occurrences underwent curation and cleaning following the ‘CoordinateCleaner’ protocol (Zizka et al. 2019), which removes records located at country and capital centroids, records from zoos and herbaria, and occurrences placed in oceanic areas. We further cropped GBIF data to retain only occurrences within the species’ native ranges. After filtering, 8887056 raw GBIF occurrences were reduced to 1878496 records. BIOTA data, already filtered, provided an additional 359036 occurrences.

Climatic data

For climatic data, we used the 19 bioclimatic variables available in the CHELSA and CanaryClim datasets (Karger et al. 2017, 2021, Patiño et al. 2023). These gridded bioclimatic variables represent yearly, seasonal, and monthly means and extremes in temperature and precipitation and have become a well-established standard for ecological modelling, macroecology, and biogeography (Guisan et al. 2017). In our study, we therefore retrieved two different climate datasets depending on the geographic context. For the non-Canarian range, we extracted present-day variables from CHELSA ver. 2.0 (Karger et al. 2017, 2021) at a 30 arc-second resolution (~ 1 km). For the Canary Islands range, we utilized the CanaryClim ver. 1.0 dataset (Patiño et al. 2023), a downscaled version of CHELSA tailored for the archipelago. The high habitat heterogeneity of small and topographically complex islands requires the use of datasets with the highest possible spatial resolution (Berio-Fortini et al. 2022, Patiño et al. 2023). Consequently, we aimed for an optimal compromise between the spatial resolutions of the climatic data and species occurrences (Chauvier et al. 2022) and resampled all CanaryClim climatic layers to a 500 × 500 m grid to ensure consistency with the BIOTA species occurrence data.

Phylogenetic distance inference

We constructed species-level backbone phylogenetic trees for each of the 82 genera considered in the present study (Supporting information). We used the ‘V.PhylMaker2’ R package (www.r-project.org) (Jin and Qian 2022), which uses the seed plant mega-phylogeny by Smith and Brown (2018) to select a given set of species. Species absent from the backbone (hereafter referred to as unplaced species, UPS; see the Supporting information) were assigned positions through 100 random placements based on additional phylogenetic or morphological information, using the ‘randtip’ R package (Ramos-Gutiérrez et al. 2023). We first identified the most derived consensus clades or singletons at the infrageneric level, to which species were randomly assigned either at the most recent common ancestor clade or at a random point along the singleton’s branch. Details on clade assignments are provided in the Supporting information. These backbone trees were then employed to calculate phylogenetic distances, defined as the sum of branch lengths (patristic distances) between pairs of introduced and native species within each genus. For each UPS, distances were calculated as the mean patristic distance across all inferred topologies (Ramos-Gutiérrez et al. 2023).

Climatic niche analyses

We used a two-step complementary modelling approach to assess differences in realized climatic niches at inter- and intraspecific levels (Fig. 1).

At the interspecific level, we quantified realized climatic niche overlap between congeneric native and introduced species pairs. Climatic niches were characterized within a reduced environmental space defined by an environmental principal component analysis of climatic variables (PCA-env; Broennimann et al. 2012). For each species separately, a PCA-env was calibrated using all pixels of the raster maps of the 19 standardized bioclimatic variables pooled between the native and invaded range, and occurrence data from the two ranges were then projected within it. Species-specific realized climatic niches were then estimated using kernel density smoothing of occurrence densities (Worton 1989), implemented in the ‘ecospat’ R package (di Cola et al. 2017, Broennimann et al. 2026), reducing artifacts related to grid resolution and sampling effort (Broennimann et al. 2012, Guisan et al. 2012). Climatic niche overlap for each congeneric native–introduced species pair was quantified using Schoener’s D, calculated from smoothed niche distributions and along the first two PCA axes, which capture the main climatic gradients (Graham et al. 2004). In total, we performed 182 pairwise comparisons involving 106 native species, as multiple introduced species within a genus could share the same closest native congener in the Canary Islands.

At the intraspecific level, we compared realized climatic niches between native and invaded ranges for 120 introduced species. Using the same specific PCA-env framework described above, occurrences from each range were projected into the reduced climatic space, and range-specific climatic envelopes were estimated via kernel density smoothing in the ‘ecospat’ R package (di Cola et al. 2017, Broennimann et al.

2026). Following Guisan et al. (2014) and Riera et al. (2025), we quantified three metrics describing range-specific realized climatic niche relationships within analogous climatic space: 1) niche expansion, E , defined as the proportion of the introduced realized climatic niche occurring outside the occupied native niche; 2) niche stability, S_e , defined as the proportion of the introduced niche overlapping the occupied native niche; and 3) niche unfilling, U , defined as the proportion of the native realized climatic niche that remains unoccupied in the invaded range despite the availability of analogous climatic conditions.

Metrics describing non-analogous climatic conditions, such as pioneering and abandonment (sensu Atwater et al. 2018 and Riera et al. 2025) were not analysed because their interpretation relative to realized versus fundamental niches under novel climates remains uncertain (Guisan et al. 2012, Chevalier et al. 2024). We use the term 'climatic niche shift' for cases where $E=1$ and $S_e=0$, following Broennimann et al. (2007, 2012), as complete occupation of novel climatic space without overlap with the native niche necessarily indicates a shift in niche position rather than a change in niche breadth alone (Guisan et al. 2014, Atwater et al. 2018). However, it is important to note that the term 'climatic niche shifts' has more generally included all other cases where the niche centroid changes without a complete occupation of novel climates (Broennimann et al. 2007, Petitpierre et al. 2012).

Statistical analyses

To test our two main hypotheses (Fig. 1), the DPAH and CMH, we used a generalized linear mixed modelling (GLMM) framework. The DPAH was evaluated through interspecific analyses of the relationship between climatic overlap and phylogenetic distance. In contrast, the CMH was assessed using intraspecific comparisons of realized climatic niche differences between native and invaded ranges, quantified primarily through niche expansion, E . Climatic niche stability, S_e and niche unfilling, U , were calculated but not modelled since: 1) S_e is, to some extent, mathematically complementary to expansion within analogous climatic space, and therefore negatively correlated with it; and 2) U mainly reflects properties of the native realized niche rather than processes occurring in the invaded range, providing limited direct inference for our focal hypotheses. To test our predictions, we focused on the effect of biogeographic origin, phylogenetic relatedness, and invasion stage, while acknowledging that additional factors (e.g. species traits, life form, residence time) may also influence invasion outcomes (Cao Pinna et al. 2025, Riera et al. 2025).

More specifically, we assessed whether climatic overlap between native and introduced congeneric species pairs (measured as Schoener's D) was influenced by phylogenetic distance (PD), biogeographic origin (i.e. Mediterranean Basin, MED; temperate Europe, EUR; Neotropics, NEO; or other Mediterranean-type regions, MET), and invasion stage (IS, i.e. naturalized versus invasive). Climatic overlap was used as response variable (1) and modelled using an ordered

beta distribution, appropriate for bounded proportional data (Kubinec 2023). GLMMs were implemented using the 'glmmTMB' R package (Brooks et al. 2017), and model diagnostics (normality and homoscedasticity of residuals) were evaluated using the 'DHARMa' R package (Barreto et al. 2021, Hartig et al. 2024). To assess whether accounting for the hierarchical structure imposed by the genus was necessary, we evaluated genus as a random effect using intra-class correlation coefficients (ICC), likelihood ratio tests (LRT), and Akaike's information criterion for small samples (AIC_c). The full GLMM (i) was compared to a nested generalized linear model (GLM) excluding the random factor using the 'lme4' R package (Zeileis and Hothorn 2002, Lüdtke et al. 2021).

ClimaticOverlap $\sim$ PD + MED + EUR + NEO

$$+ \text{MET} + \text{IS} + (1 \mid \text{Genus}) \quad (1)$$

To disentangle the relative influence of phylogenetic distance, biogeographic origin, and the invasion stage, we used the *dredge* function in the 'MuMIn' R package (Barton 2025) to generate all possible combinations of predictor variables. Model selection was based on the corrected AIC_c, with models ranked by ΔAIC_c . Models with $\Delta\text{AIC}_c \leq 2$ relative to the best-supported model were considered equally supported and effectively indistinguishable in model fit (Burnham and Anderson 2010). To assess the robustness of the results, analyses were repeated using a reduced dataset excluding UPSs.

Second, to test CMH at the intraspecific level, we modelled expansion (2) as response variable, again using ordered beta distributions. Predictor variables included biogeographic origin (presence/absence in the Mediterranean Basin, temperate Europe, Neotropics, or other Mediterranean-type regions) and invasion stage (naturalized versus invasive). As above, we evaluated the inclusion of genus as a random factor:

Expansion $\sim$ MED + EUR + NEO

$$+ \text{MET} + \text{IS} + (1 \mid \text{Genus}) \quad (2)$$

We applied the same model selection procedure described above, constructing all possible combinations of predictor variables and identifying supported models using the $\Delta\text{AIC}_c \leq 2$ threshold (Burnham and Anderson 2010). Model diagnostics were assessed using the 'DHARMa' R package. To disentangle the relative importance of biogeographic origin and invasion stage, we generated model-averaged estimates from the supported models, interpreting standardized coefficients and summed model weights (sw) provided by 'MuMIn'. All analyses were performed on the Teide High-Performance Computing facility (TEIDE-HPC) operated by Instituto Tecnológico y de Energías Renovables (ITER, S.A.).

Results

Climate description and biogeographic origins

We compiled a dataset comprising 631 species across 97 genera, including 268 introduced species. Although a subset of genera was excluded from downstream analyses (Material and methods), we provide a general overview of the climatic and biogeographic affinities of all introduced species. Most introduced species originated from temperate (54.5%) and subtropical (27.9%) climatic zones, with smaller proportions from dry tropical (10.1%), wet tropical (3.7%), and desert climatic zones (3.7%, Fig. 2B). Biogeographically, the Mediterranean Basin was the dominant source region, accounting for 35.8%, followed by temperate Europe (14.2%) and the Neotropics (13.1%) (Fig. 2B). A notable proportion of species (13.4%) were classified as widespread, while the remaining taxa originated from temperate Asia (6.3%), tropical Africa (6.3%), Cape Region (5.2%), the Nearctic (2.6%), Australasia (2.2%), and tropical Asia (0.7%) (Fig. 2B, Supporting information).

Phylogenetic uncertainty and distance

Of the 82 genera retained for analysis (see Occurrence data), 160 native or introduced species were absent from the backbone phylogeny. Twenty-six of these were identified as taxonomic synonyms. The remaining UPS were then integrated into the tree using 100 random placements based on available morphological and phylogenetic information. Among these, 31 were assigned as sister species or singletons, while 103 were placed within the most derived consensus clades supported by prior studies (Supporting information).

Phylogenetic distances between introduced and native congeners varied by biogeographic region (Fig. 2C). Introduced species from the Mediterranean Basin and temperate Europe showed significantly shorter phylogenetic distances to native Canarian species than those introduced from other regions (both $p < 0.05$, Fig. 2C). In contrast, Neotropical introduced congeners showed significantly greater phylogenetic distances to their native counterparts compared to species from other regions ($p < 0.05$, Fig. 2C). No significant differences were observed for species originating from other Mediterranean-type climate regions compared to species from other biogeographic regions ($p > 0.05$, Fig. 2C).

Climate overlap at the interspecific level

Overall, climatic overlap between introduced species and their nearest native congeners was low, regardless of biogeographic origin (Fig. 2D, Supporting information). LRTs and AIC_c indicated that the GLMM approach, which included genus as a random factor, provided a significantly better fit to the data than the nested GLM without a random effect ($\chi^2 = 30.5$, $p < 0.001$, $\Delta AIC_c = 28.2$). Additionally, ICC showed that a moderate portion of the variance was explained by within-genus comparisons ($ICC = 0.254$).

Models testing for pre-adaptation, specifically those including phylogenetic distance as a predictor of climatic overlap, received limited statistical support. Model comparison showed that the null model had the lowest AIC_c value, but models including MED, NEO, or PD were within $\Delta AIC_c < 2$ (Table 1). This indicates that none of the predictors provided a clear improvement to any model over the null model, although remaining within the set of plausible models. These results remained robust when using those datasets where UPS were not considered (Supporting information).

Intraspecific differences in realized climatic niches

Of the 120 introduced species included in the intraspecific analyses, 41 (34%) occupied climatic space entirely outside their occupied native realized niche (expansion $[E] = 1$, stability $[S_c] = 0$), and were therefore classified as exhibiting climatic niche shifts. An additional 77 (64%) species showed high climatic niche expansion values (≥ 0.75). Mean values ($\pm$ SD) of climatic niche E and U per species were high (0.71 ± 0.37 and 0.86 ± 0.25 , respectively), whereas S_c was consistently lower (0.21 ± 0.32 ; Supporting information). Eight species exhibited invaded ranges restricted to non-analogous climatic conditions, for which expansion and stability could not be quantified within analogous climate space ($E = 0$ versus $S_c = 0$; Supporting information). These eight species were therefore excluded from subsequent modelling. Variability among species grouped by biogeographic origin was also evident, although differences were not statistically significant (Supporting information).

For models testing the CMH, LRTs indicated no significant effect of genus on climatic niche expansion ($\chi^2 = 0.13$, n.s.), and ICC values were low ($ICC = 0.136$). Accordingly, genus was excluded from the final models. Model selection based on ΔAIC_c identified five supported models for climatic niche expansion (Supporting Information). Model averaging

Table 1. Model selection of the generalized linear mixed models predicting climatic overlap between introduced and native congeneric species as a function of phylogenetic distance (PD), the presence in the Mediterranean Basin (MED), Temperate Europe (EUR), Neotropics (NEO), and/or Mediterranean-type climates (MET), as well as the invasion stage. All possible combinations of models were ranked using ΔAIC_c , while only models with $\Delta AIC_c \leq 2$ are reported. Model: includes all of the selected subsets of models; Log(L): maximized log-likelihood; ΔAIC_c : difference between AIC_c compared with the best-ranked model

Model	log(L)	df	AIC_c	ΔAIC_c
Climatic overlap ~ 1 + (1 genus)	138.92	5	-267.5	0
Climatic overlap ~ MED + (1 genus)	139.53	6	-266.6	0.9
Climatic overlap ~ MED + NEO + (1 genus)	140.42	7	-266.2	1.3
Climatic overlap ~ NEO + (1 genus)	139.19	6	-265.9	1.6
Climatic overlap ~ PD + (1 genus)	139.07	6	-265.7	1.8
Climatic overlap ~ MET + (1 genus)	138.99	6	-265.5	2.0

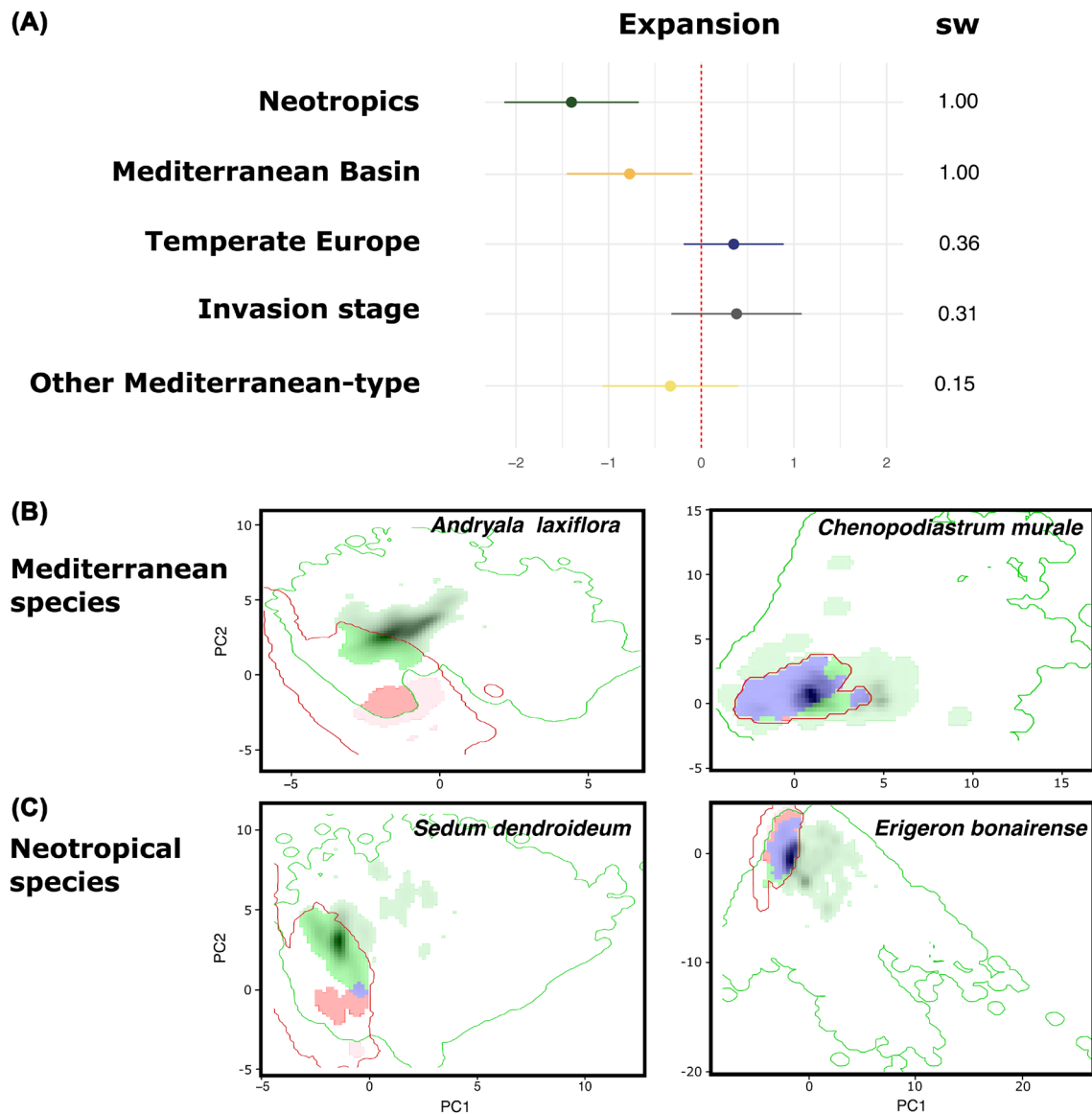


Figure 3. Importance of biogeographic origin and invasion stage for the realized climatic niche metrics. (A) The importance of biogeographic origin (presence of a species as native in a given region) and invasion stage (naturalized versus invasive) for climatic niche expansion based on the sum of model weights (sw) from averaged GLMs ($n = 112$). Coefficients to the left of the red vertical line (zero) indicate negative relationships with the response variable (i.e. lower expansion values) for species native to a given biogeographic region or classified as naturalized; coefficients to the right of the red line indicate positive relationships. (B) and (C) Examples of species-specific realized climatic niches (PCA-env) for the two biogeographic regions showing significant effects, the Mediterranean Basin (B) and the Neotropics (C). Native and invaded ranges are shown in green and red, respectively, with niche overlap shown in purple. Examples on the right (*Chenopodium murale*, *Erigeron bonariense*) correspond to species with high climatic niche stability and low expansion, whereas examples on the left (*Andryala laxiflora*, *Sedum dendroideum*) represent species with high expansion and low stability.

retained biogeographic origin and invasion stage as relevant predictors, although their influence differed. The Neotropics and Mediterranean Basin showed the highest summed model weights ($sw = 1$ for both, Fig. 3). Standardized coefficients indicated that niche expansion was negatively associated with native presence in the Neotropics and, to a lesser extent, the Mediterranean Basin (Fig. 3A; Supporting information). In contrast, native presence in temperate Europe, other Mediterranean-type regions, and invasion stage showed

no significant association with this metric (Supporting information).

Discussion

By integrating phylogenetic relationships with distribution data from both native and introduced congeneric species, we independently tested both the DPAH and the CMH.

Interspecific comparisons between congeneric species did not support the DPAH, challenging the underlying phylogenetic niche conservatism hypothesis, according to which introduced species are more likely to establish if they share adaptive, heritable traits, and hence are closely related to their native counterpart. We found evidence supporting the CMH at the intraspecific level, indicating that climate matching plays a role in the invasion success of species from both the Mediterranean Basin and the Neotropics. However, extensive climatic niche expansion throughout the different groups challenges the strict interpretation of the CMH.

Biogeographic origins and phylogenetic relatedness of introduced flora

Introduced species that are congeneric to natives in the Canary Islands originate predominantly from temperate and subtropical climate zones, particularly the Mediterranean Basin and temperate Europe. At first sight, this pattern aligns with two key expectations: 1) a relatively high macroclimatic match between native and invaded ranges, potentially reinforcing the role of inter- and intraspecific niche conservatism as a main driver of establishment and invasion (Wiens and Graham 2005, Petitpierre et al. 2012, Strubbe et al. 2015, Liu et al. 2020, Broennimann et al. 2021; but see Stroud 2021); and 2) the Mediterranean Basin as a key donor region to other areas with a Mediterranean-type climate (Kalusov   et al. 2017, Casado et al. 2018, Cao Pinna et al. 2021). Long-standing human–plant interactions in Mediterranean and European landscapes likely facilitated adaptation to anthropogenic environments, thereby increasing invasion potential (Di Castri 1989, Jeschke and Strayer 2005, Hierro et al. 2006, Kalusov   et al. 2017, McDougall et al. 2018). However, these trends are limited to the subset of species chosen because they have congeneric native species present in the islands and may not extend to the entire naturalized and invasive flora of the Canary Islands (Morente-L  pez et al. 2023). Identifying the mechanisms underlying these patterns therefore remains both a key challenge and an opportunity to refine predictions of plant invasions (Py  sek et al. 2015, van Kleunen et al. 2018, Gioria et al. 2023).

Limited climatic niche support for Darwin’s pre-adaptation hypothesis

In the subset of species analysed, Mediterranean and temperate European introduced species are phylogenetically closer to native Canarian species than species from other regions, consistent with patterns described for the assembly of native vascular flora (Carine et al. 2010, Mart  n-Hernanz et al. 2023, reviewed by Fern  ndez-Palacios et al. 2024). Our analyses provided only limited support for an effect of PD or biogeographic origin on climatic niche overlap. The null model had the lowest AIC_c value, but models including MED, NEO, or PD also fell within the set of plausible models, indicating that these predictors cannot be entirely ruled out, even though they did not provide a clear improvement in explanatory power. Overall, these results provide little support for the DPAH and suggest that climatic niche

conservatism is not a universal mechanism promoting invasion success among close relatives (Park et al. 2020, Qian and Sandel 2022). Instead, its influence appears to be context-dependent and contingent on both evolutionary trajectories and regional ecological circumstances.

These results contrast with broader-scale studies that link pre-adaptation with invasion success (Park and Potter 2015, Park et al. 2020, Qian and Sandel 2022, 2023). Several factors may explain this discrepancy. At fine evolutionary and spatial scales, such as genus-level comparisons within a single archipelago, phylogenetic dispersion can vary widely, obscuring potential relationships with climatic overlap by leading to increased phylogenetic clustering, dispersion, or neither (Cadotte et al. 2009, Qian and Sandel 2022, 2023). Thus, support for the phylogenetic niche conservatism hypothesis may arise when phylogenetic distances between native and introduced species are computed at macroevolutionary scales, as for instance across the entire phylogeny of species present in a given region (Qian et al. 2022). Indeed, deep branches may contribute more than shallow branches among congeneric species in characterizing phylogenetic niche conservatism (Hardy et al. 2012).

Spatial niche truncation due to sampling biases or restricted climatic ranges, often invoked as a driver of inaccurate predictions of species distributions (Guisan et al. 2014, Chevalier et al. 2021), can further obscure potential patterns by adding noise to estimates of the relationship between climatic overlap and phylogenetic relatedness. Complementing DPAH, the ‘niche preemption’ hypothesis proposes that the presence of native congeners could limit the establishment of newly arriving closely related lineages through priority effects (Silvertown 2004), whereas ‘Darwin’s naturalization’ hypothesis predicts the success of introduced species that are not closely related to the native species (Diez et al. 2008). While our results could point towards these hypotheses, our methodology does not directly test them, as the underlying processes involve biotic resistance and competitive exclusion rather than niche or trait similarities (Cadotte et al. 2018). Regardless, these findings emphasize the complementary role to interspecific approaches to intraspecific comparisons of realized climatic niches when testing invasion hypotheses such as DPAH (Haubrock et al. 2024).

On the role of differences in realized climatic niches

In our study, climatic niche expansion was widespread among introduced species, whereas niche stability remained generally low. Over one-third of species (34%) exhibited climatic niche shifts, occupying climatic space entirely outside the realized niche occupied across their native range, and a further 30% showed high expansion values (≥ 0.75). Across biogeographic origins, descriptive patterns consistently indicated low stability and comparatively high expansion and unfilling. Model selection analyses further identified biogeographic origin as a key predictor of expansion, with species of Neotropical and Mediterranean Basin origin showing lower expansion.

These convergent responses across contrasting biogeographic origins likely reflect the strong climatic heterogeneity

of the Canary Islands, driven by steep altitudinal gradients, complex topography, and proximity to Africa (del Arco-Aguilar and Rodríguez-Delgado 2018, Patiño et al. 2023), which generate climatic conditions analogous to both Mediterranean and Neotropical semi-arid regions. Climatic matching between native and invaded ranges, reflected in higher stability values, likely facilitates naturalization and spread, particularly among xerophytic species adapted to seasonal drought through diverse functional strategies (Gianoli and Molina-Montenegro 2021, Ferreras et al. 2023). However, attributing invasion success solely to climatic matching, and thus to partial support for the CMH, would oversimplify the underlying processes. Recent studies in Mediterranean systems instead emphasize the roles of long-distance dispersal, novel biotic interactions, and local acclimation in driving climatic niche shifts (Cao Pinna et al. 2025), whereas niche conservatism appears more strongly associated with longer residence times and broader native climatic niches (Riera et al. 2025).

Understanding introduced niches beyond climate matching

Although limited by our modelling approach, our findings reinforce previous evidence that climatic niche changes (i.e. expansion or shift) are common in biological invasions (Petitpierre et al. 2012, Liu et al. 2020), with or without modification of the fundamental niche (Broennimann et al. 2007, 2014, Guisan et al. 2014, Tingley et al. 2014, Colautti et al. 2016). Many introduced species appear to occupy climatic conditions absent in their native ranges (Pearman et al. 2008, Gallagher et al. 2010), thus facilitating occupation of non-analogous climatic regimes. Recent evidence further suggests that 65–100% of 815 terrestrial plant species introduced across five continents have undergone climatic niche shifts, depending on how these shifts were measured (Atwater and Barney 2021). The climatic niche shift detected for a subset of species may result from ecological release from natural or anthropogenic biotic constraints (e.g. interspecific competition, predation, pathogens, pests) or dispersal limitations in the native range (Catford et al. 2011, van Kleunen et al. 2018, Gioria et al. 2023). The relatively high proportion of congeneric species compared with the full introduced flora may also be interpreted as evidence against the ‘niche pre-emption’ hypothesis (Silvertown 2004). Originally developed to explain establishment versus exclusion under natural assembly processes, this hypothesis can be extended to invasion contexts, where the presence of closely related native congeners would be expected to preclude the establishment of exotic congeners through priority effects (Pulliam and Danielson 1991, Fraser et al. 2015). This prediction was not supported by our results.

Alternatively, climatic niche shifts may arise from rapid in situ evolution, leading to changes in species’ fundamental niche tolerances (Kubisch et al. 2013, Wiens et al. 2019). Besides this, climatic mismatch may also reflect spread lags, whereby introduced species have not yet occupied their full potential climatic space (Petitpierre et al. 2012). In other

words, a lag between colonization and complete range shift can occur, influenced by residence time and other intrinsic or extrinsic factors (Wilson et al. 2007, Gioria et al. 2023, Robeck et al. 2024, Riera et al. 2025). This phenomenon, often termed ‘invasion debt’ (Essl et al. 2011, Cao Pinna et al. 2024), could partly explain the relatively high levels of niche unfilling observed in our analyses. However, because we did not explicitly quantify the availability of native-range climatic space within the Canary Islands, niche unfilling cannot be attributed unambiguously to invasion debt alone. These lags further complicate predictions of future spread and invasion events (Sax et al. 2007) and highlight the need for ongoing monitoring and integrative early-detection approaches, including mapping, surveillance, and scanning exercises (Simberloff et al. 2013, Hulme 2025).

While this study provides valuable insights into differences in realized climatic niches, an important limitation remains: cloud cover and mist precipitation, key drivers of plant distributions in the Canary Islands (Sperling et al. 2004, Marzol 2008, García-Alvarado et al. 2024), are not explicitly represented in CanaryClim or CHELSA. As a result, some inferred climatic niche expansion may reflect the exploitation of suitable microclimatic conditions not captured by these climatic datasets. Future work should integrate satellite-derived information on cloud cover and inversion-layer height (Pouteau et al. 2018, Dorta-Antequera and Correa González 2025) with existing bioclimatic datasets to better represent these critical environmental drivers and clarify their role in plant establishment and invasion (Steen et al. 2024).

Overall, many introduced species appear far from climatic equilibrium in their invaded ranges, indicating potential for continued range expansion under ongoing climatic and environmental change (Wallingford et al. 2020, Naimi et al. 2022, Gioria et al. 2023). Land-use change has likewise been identified as a major driver of biological invasions in the Canary Islands (Fernández-Palacios et al. 2023). Because our estimates of realized climatic niches are derived from restricted temporal and spatial windows (i.e. reflecting occurrence and climate data spanning only recent decades, Atwater et al. 2018), future research should adopt broader temporal and geographic scales, incorporate more comprehensive phylogenetic frameworks, and integrate non-climatic predictors (e.g. historical and contemporaneous land-use change). Such approaches will better capture the complexity of plant invasions and realized niche changes during naturalization at both inter- and intraspecific levels (Cadotte et al. 2018, Lovell et al. 2021, Maitner et al. 2022).

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Author contributions

Louis S. Jay-García: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Yurena Arjona:** Conceptualization (supporting); Formal analysis (supporting); Methodology (equal); Software (supporting); Supervision (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Flavien Collart:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (supporting); Methodology (equal); Software (supporting); Supervision (equal); Writing – review and editing (equal). **Alain Vanderpoorten:** Conceptualization (supporting); Formal analysis (supporting); Methodology (equal); Writing – review – editing (equal). **Antoine Guisan:** Methodology (equal); Resources (equal); Software (equal); Writing – review – editing (equal). **Olivier Broennimann:** Data curation (equal); Methodology (supporting); Software (equal); Writing – review – editing (equal). **José María Fernández-Palacios:** Funding acquisition (equal); Project administration (equal); Supervision (equal); Writing – review – editing (equal). **Jairo Patiño:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (supporting); Software (supporting); Supervision (equal); Visualization (supporting); Writing – original draft (lead); Writing – review – editing (equal).

Data availability statement

Data and Code are available from the Figshare Digital Repository: <https://doi.org/10.6084/m9.figshare.28844219> (Jay-García et al. 2026). Occurrence data can be found in two public repositories: Canary Island Occurrence data was obtained from the Biodiversity Data Bank of the Canary Islands, BIOTA (Gobierno de Canarias, 2023), and can be retrieved from <https://www.biodiversidadcanarias.es/biota/analisis/mapas/> Native-range (non-Canarian) data was obtained from GBIF (2023) and can be retrieved from: [10.15468/dl.hpugsgs](https://doi.org/10.15468/dl.hpugsgs) [10.15468/dl.rfxudz](https://doi.org/10.15468/dl.rfxudz) [10.15468/dl.yfmksy](https://doi.org/10.15468/dl.yfmksy) [10.15468/dl.a4p45b](https://doi.org/10.15468/dl.a4p45b) [10.15468/dl.p7kfcmm](https://doi.org/10.15468/dl.p7kfcmm) [10.15468/dl.v9hxn](https://doi.org/10.15468/dl.v9hxn).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Adler, G. H. and Levins, R. 1994. The island syndrome in rodent populations. – *Q. Rev. Biol.* 69: 473–490.
- Atwater, D. Z. and Barney, J. N. 2021. Climatic niche shifts in 815 introduced plant species affect their predicted distributions. – *Global Ecol. Biogeogr.* 30: 1671–1684.
- Atwater, D. Z., Ervine, C. and Barney, J. N. 2018. Climatic niche shifts are common in introduced plants. – *Nat. Ecol. Evol.* 2: 34–43.
- Barreto, E., Rangel, T. F., Pellissier, L. and Graham, C. H. 2021. Area, isolation and climate explain the diversity of mammals on islands worldwide. – *Proc. R. Soc. B Biol. Sci.* 288: 20211879.
- Bartoň, K. 2025. MuMIn: multi-model inference. – R package ver. 1.48.19, <https://CRAN.R-project.org/package=MuMIn>.
- Bates, O. K. and Bertelsmeier, C. 2021. Climatic niche shifts in introduced species. – *Curr. Biol.* 31: R1252–R1266.
- Bellard, C., Cassey, P. and Blackburn, T. M. 2016. Alien species as a driver of recent extinctions. – *Biol. Lett.* 12: 20150623.
- Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U. and Richardson, D. M. 2011. A proposed unified framework for biological invasions. – *Trends Ecol. Evol.* 26: 333–339.
- Broennimann, O., Treier, U. A., Müller-Schärer, H., Thuiller, W., Peterson, A. T. and Guisan, A. 2007. Evidence of climatic niche shift during biological invasion. – *Ecol. Lett.* 10: 701–709.
- Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N. E., Graham, C. H. and Guisan, A. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. – *Global Ecol. Biogeogr.* 21: 481–497.
- Broennimann, O., Mráz, P., Petitpierre, B., Guisan, A. and Müller-Schärer, H. 2014. Contrasting spatio-temporal climatic niche dynamics during the eastern and western invasions of spotted knapweed in North America. – *J. Biogeogr.* 41: 1126–1136.
- Broennimann, O., Petitpierre, B., Chevalier, M., González-Suárez, M., Jeschke, J. M., Rolland, J., Gray, S. M., Bacher, S. and Guisan, A. 2021. Distance to native climatic niche margins explains establishment success of alien mammals. – *Nat. Commun.* 12: 2353.
- Broennimann, O., Collart, F. and Guisan, A. 2026. The ecospat R package: a collection of pre-, core-, and post-modeling tools to investigate species niches and distributions. – In: Rocchini, D. (ed.), *R coding for ecology. Use R!* Springer, pp. 67–98.
- Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M. and Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – *R J.* 9: 378–400.
- Brummitt, R. K. 2001. World geographic scheme for recording plant distributions. – Hunt Institute for Botanical Documentation Carnegie Mellon Univ.
- Burnham, K. P. and Anderson, D. R. 2010. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.
- Burns, K. C. 2019. Evolution in isolation: the search for an island syndrome in plants. – Cambridge Univ. Press.
- Cadotte, M. W., Hamilton, M. A. and Murray, B. R. 2009. Phylogenetic relatedness and plant invader success across two spatial scales. – *Divers. Distrib.* 15: 481–488.

- Cadotte, M. W., Campbell, S. E., Li, S., Sodhi, D. S. and Mandrak, N. E. 2018. Preadaptation and naturalization of nonnative species: Darwin's two fundamental insights into species invasion. – *Annu. Rev. Plant Biol.* 69: 661–684.
- Cao Pinna, L., Axmanová, I., Chytrý, M., Malavasi, M., Acosta, A. T. R., Giulio, S., Attorre, F., Bergmeier, E., Biurrun, I., Campos, J. A., Font, X., Kůzmič, F., Landucci, F., Marcenò, C., Rodríguez-Rojo, M. P. and Carboni, M. 2021. The biogeography of alien plant invasions in the Mediterranean Basin. – *J. Veg. Sci.* 32: e12980.
- Cao Pinna, L., Gallien, L., Pollock, L. J., Axmanová, I., Chytrý, M., Malavasi, M., Acosta, A. T. R., Campos, J. A. and Carboni, M. 2024. Plant invasion in Mediterranean Europe: current hotspots and future scenarios. – *Ecography* 2024: e07085.
- Cao Pinna, L., Gallien, L., Jucker, T., Chytrý, M., La Bella, G., Acosta, A. T. R. and Carboni, M. 2025. Niche dynamics of alien plant species in Mediterranean Europe. – *Global Change Biol.* 31: e70379.
- Carine, M. and Sequeira, M. 2020. Sir Joseph Hooker on insular floras: human impact and the natural laboratory paradigm. – *Sci. Insul.* 3: 73–88.
- Carine, M. A., Santos-Guerra, A., Guma, I. R. and Reyes-Betancort, J. A. 2010. Endemism and evolution of the Macaronesian flora. – In: Knapp, S. (ed.), *Beyond cladistics: the branching of a paradigm*. Univ. of California Press. 101–124.
- Carlquist, S. J. 1974. *Island biology*. – Columbia Univ. Press.
- Casado, M. A., Martín-Forés, I., Castro, I., de Miguel, J. M. and Acosta-Gallo, B. 2018. Asymmetric flows and drivers of herbaceous plant invasion success among Mediterranean-climate regions. – *Sci. Rep.* 8: 16834.
- Catford, J. A., Vesk, P. A., White, M. D. and Wintle, B. A. 2011. Hotspots of plant invasion predicted by propagule pressure and ecosystem characteristics. – *Divers. Distrib.* 17: 1099–1110.
- Caujapé-Castells, J., Tye, A., Crawford, D. J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Vincent Florens, F. B., Moura, M. and Jardim, R. 2010. Conservation of oceanic island floras: present and future global challenges. – *Perspect. Plant Ecol. Evol. Syst.* 12: 107–129.
- Chauvier, Y., Descombes, P., Guéguen, M., Boulangeat, L., Thuiller, W. and Zimmermann, N. E. 2022. Resolution in species distribution models shapes spatial patterns of plant multifaceted diversity. – *Ecography* 2022: e05973.
- Chevalier, M., Broennimann, O., Cornuault, J. and Guisan, A. 2021. Data integration methods to account for spatial niche truncation effects in regional projections of species distribution. – *Ecol. Appl.* 31: e02427.
- Chevalier, M., Broennimann, O. and Guisan, A. 2024. Climate change may reveal currently unavailable parts of species' ecological niches. – *Nat. Ecol. Evol.* 8: 1298–1310.
- Colautti, R. I. and Lau, J. A. 2016. Contemporary evolution during invasion. – In: Barrett, S. C. H. et al. (eds), *Invasion genetics*. John Wiley and Sons Ltd, pp. 101–121.
- Cronk, Q. C. B. and Fuller, J. L. 2014. *Plant invaders: the threat to natural ecosystems*. – Routledge.
- Daehler, C. 2001. Darwin's naturalization hypothesis revisited. – *Am. Nat.* 158: 324–330.
- Dai, Z.-C., Wan, L.-Y., Qi, S.-S., Rutherford, S., Ren, G.-Q., Wan, J. S. H. and Du, D.-L. 2020. Synergy among hypotheses in the invasion process of alien plants: a road map within a timeline. – *Perspect. Plant Ecol. Evol. Syst.* 47: 125575.
- Daru, B. H., Davies, T. J., Willis, C. G., Meineke, E. K., Ronk, A., Zobel, M., Pärtel, M., Antonelli, A. and Davis, C. C. 2021. Widespread homogenization of plant communities in the Anthropocene. – *Nat. Commun.* 12: 6983.
- Darwin, C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. – John Murray.
- Dawson, W. et al. 2017. Global hotspots and correlates of alien species richness across taxonomic groups. – *Nat. Ecol. Evol.* 1: 1–7.
- del Arco-Aguilar, M. J. and Rodríguez-Delgado, O. 2018. *Vegetation of the Canary Islands*. – Springer.
- Di Castri, F. 1989. History of biological invasions with special emphasis on the old world. – In: Drake, J. A. et al. (eds), *Biological invasions: a global perspective*. Wiley and Sons, Ltd, pp. 1–30.
- Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., D'Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, L., Mateo, R. G., Hordijk, W., Salamin, N. and Guisan, A. 2017. *Ecospat*: an R package to support spatial analyses and modeling of species niches and distributions. – *Ecography* 40: 774–787.
- Diez, J. M., Sullivan, J. J., Hulme, P. E., Edwards, G. and Duncan, R. P. 2008. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. – *Ecol. Lett.* 11: 674–681.
- Donlan, C. J., Terschy, B. R., Campbell, K. and Cruz, F. 2003. Research for requiems: the need for more collaborative action in eradication of invasive species. – *Conserv. Biol.* 17: 1850–1851.
- Dorta-Antequera, P. and Correa-González, J. 2025. Methodological approach for the characterisation and trend analysis of subsidence thermal inversions: the case of the Canary Islands. – *Int. J. Climatol.* 45: e8933.
- Duncan, R. P. and Williams, P. A. 2002. Darwin's naturalization hypothesis challenged. – *Nature* 417: 608–609.
- Early, R. and Sax, D. F. 2014. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. – *Global Ecol. Biogeogr.* 23: 1356–1365.
- Enders, M. et al. 2020. A conceptual map of invasion biology: integrating hypotheses into a consensus network. – *Global Ecol. Biogeogr.* 29: 978–991.
- Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Hülber, K., Jarošík, V., Kleinbauer, I., Krausmann, F., Kühn, I., Nentwig, W., Vilà, M., Genovesi, P., Gherardi, F., Desprez-Loustau, M.-L., Roques, A. and Pyšek, P. 2011. Socioeconomic legacy yields an invasion debt. – *Proc. Natl. Acad. Sci.* 108: 203–207.
- Fernández-Palacios, J. M., Schrader, J., de Nascimento, L., Irl, S. D. H., Sánchez-Pinto, L. and Otto, R. 2023. Are plant communities on the Canary Islands resistant to plant invasion?. – *Divers. Distrib.* 29: 51–60.
- Fernández-Palacios, J. M., Otto, R., Capelo, J., Caujapé-Castells, J., De Nascimento, L., Duarte, M. C., Elias, R. B., García-Verdugo, C., Menezes De Sequeira, M., Médail, F., Naranjo-Cigala, A., Patiño, J., Price, J., Romeiras, M. M., Sánchez-Pinto, L. and Whittaker, R. J. 2024. In defence of the entity of Macaronesia as a biogeographical region. – *Biol. Rev.* 99: 2060–2081.
- Ferreras, A. E., Ashworth, L. and Giorgis, M. A. 2023. Uncoupled flowering and fruiting phenology as the strategy of non-native invasive woody species in seasonally dry ecosystems. – *Biol. Invasions* 25: 365–377.
- Florencio, M. et al. 2021. Macaronesia as a fruitful arena for ecology, evolution, and conservation biology. – *Front. Ecol. Evol.* 9: 718169.

- Fortini, L. B., Kaiser, L. R., Xue, L. and Wang, Y. 2022. Bioclimatic variables dataset for baseline and future climate scenarios for climate change studies in Hawai'i. – *Data Brief* 45: 108572.
- Fraser, C. I., Banks, S. C. and Waters, J. M. 2015. Priority effects can lead to underestimation of dispersal and invasion potential. – *Biol. Invasions* 17: 1–8.
- Gallagher, R. V., Beaumont, L. J., Hughes, L. and Leishman, M. R. 2010. Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. – *J. Ecol.* 98: 790–799.
- García-Alvarado, J. J., Bello-Rodríguez, V., González-Mancebo, J. M. and Del Arco, M. J. 2024. Updating knowledge of vegetation belts on a complex oceanic island after 20 years under the effect of climate change. – *Biodivers. Conserv.* 33: 2441–2463.
- GBIF. 2023. The Global Biodiversity Information Facility. What is GBIF?. – GBIF. <https://www.gbif.org/what-is-gbif>
- Gianoli, E. and Molina-Montenegro, M. A. 2021. Evolution of physiological performance in invasive plants under climate change. – *Evolution* 75: 3181–3190.
- Gioria, M., Hulme, P. E., Richardson, D. M. and Pyšek, P. 2023. Why are invasive plants successful? – *Annu. Rev. Plant Biol.* 74: 635–670.
- Gobierno de Canarias. 2023. BIOTA: banco de datos de biodiversidad de Canarias [Occurrence dataset]. – BIOTA. <https://www.biodiversidadcanarias.es/biota/analisis/mapas>
- Gobierno de Canarias. 2025. BIOTA: estadísticas. – BIOTA Estad. <https://www.biodiversidadcanarias.es/biota/estadisticas>
- Govaerts, R., Nic Lughadha, E., Black, N., Turner, R. and Paton, A. 2021. The world checklist of vascular plants, a continuously updated resource for exploring global plant diversity. – *Sci. Data* 8: 215.
- Graham, C. H., Ferrier, S., Huettman, F., Moritz, C. and Peterson, A. T. 2004. New developments in museum-based informatics and applications in biodiversity analysis. – *Trends Ecol. Evol.* 19: 497–503.
- Guisan, A., Petitpierre, B., Broennimann, O., Kueffer, C., Randin, C. and Daehler, C. 2012. Response to comment on 'climatic niche shifts are rare among terrestrial plant invaders'. – *Science* 338: 193.
- Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C. and Kueffer, C. 2014. Unifying niche shift studies: insights from biological invasions. – *Trends Ecol. Evol.* 29: 260–269.
- Guisan, A., Thuiller, W. and Zimmermann, N. E. 2017. Habitat suitability and distribution models: with applications in R. – Cambridge Univ. Press.
- Hardy, O. J., Couteron, P., Munoz, F., Ramesh, B. R. and Péliissier, R. 2012. Phylogenetic turnover in tropical tree communities: impact of environmental filtering, biogeography and mesoclimatic niche conservatism. – *Global Ecol. Biogeogr.* 21: 1007–1016.
- Hartig, F., Lohse, L. and Leite, M. de S. 2024. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. – R package ver. 0.4.6 <http://florianhartig.github.io/DHARMA/>
- Haubrock, P. J., Cuthbert, R. N., Balzani, P., Briski, E., Cano-Barbacid, C., De Santis, V., Hudgins, E. J., Kouba, A., Macêdo, R. L., Kourantidou, M., Renault, D., Rico-Sánchez, A. E., Soto, I., Toutain, M., Tricarico, E. and Tarkan, A. S. 2024. Discrepancies between non-native and invasive species classifications. – *Biol. Invasions* 26: 371–384.
- Hierro, J. L., Villarreal, D., Eren, Ö., Graham, J. M. and Callaway, R. M. 2006. Disturbance facilitates invasion: the effects are stronger abroad than at home. – *Am. Nat.* 168: 144–156.
- Hill, M. P., Gallardo, B. and Terblanche, J. S. 2017. A global assessment of climatic niche shifts and human influence in insect invasions. – *Global Ecol. Biogeogr.* 26: 679–689.
- Hulme, P. E. 2021. Unwelcome exchange: international trade as a direct and indirect driver of biological invasions worldwide. – *One Earth* 4: 666–679.
- Hulme, P. E. 2025. Trouble on the horizon: anticipating biological invasions through futures thinking. – *Biol. Rev.* 100: 461–480.
- Hutchinson, G. E. 1957. Concluding remarks. – *Cold Spring Harb. Symp. Quant. Biol.* 22: 415–427.
- Irl, S. D. H., Schweiger, A. H., Steinbauer, M. J., Ah-Peng, C., Arévalo, J. R., Beierkuhnlein, C., Chiarucci, A., Daehler, C. C., Fernández-Palacios, J. M., Flores, O., Kueffer, C., Madêra, P., Otto, R., Schweiger, J. M.-I., Strasberg, D. and Jentsch, A. 2021. Human impact, climate and dispersal strategies determine plant invasion on islands. – *J. Biogeogr.* 48: 1889–1903.
- Jay-García, L. S., Arjona, Y., Collart, F., Vanderpoorten, A., Broenniman, O., Guisan, A., Fernández-Palacios, J. M. and Patiño, J. 2026. Data from: Moving beyond environmental filtering hypotheses – deciphering the drivers of congeneric plant introductions in an oceanic archipelago. – Figshare, <https://doi.org/10.6084/m9.figshare.28844219>.
- Jeschke, J. M. and Strayer, D. L. 2005. Invasion success of vertebrates in Europe and North America. – *Proc. Natl. Acad. Sci.* 102: 7198–7202.
- Jin, Y. and Qian, H. 2022. VPhyloMaker2: an updated and enlarged R package that can generate very large phylogenies for vascular plants. – *Plant Divers.* 44: 335–339.
- Kalusová, V., Chytrý, M., van Kleunen, M., Mucina, L., Dawson, W., Essl, F., Kreft, H., Pergl, J., Weigelt, P., Winter, M. and Pyšek, P. 2017. Naturalization of European plants on other continents: the role of donor habitats. – *Proc. Natl. Acad. Sci.* 114: 13756–13761.
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P. and Kessler, M. 2017. Climatologies at high resolution for the earth's land surface areas. – *Sci. Data* 4: 170122.
- Karger, D. N., Lange, S., Hari, C., Reyer, C. P. O. and Zimmermann, N. E. 2021. ISIMIP Repository. – CHELSA-W5E5 V10 W5E5 V10 Downscal. CHELSA V20. <https://doi.org/10.48364/ISIMIP.836809.2>
- König, C., Weigelt, P., Taylor, A., Stein, A., Dawson, W., Essl, F., Pergl, J., Pyšek, P., van Kleunen, M., Winter, M., Chatelain, C., Wieringa, J. J., Krestov, P. and Kreft, H. 2021. Source pools and disharmony of the world's island floras. – *Ecography* 44: 44–55.
- Kubinec, R. 2023. Ordered beta regression: a parsimonious, well-fitting model for continuous data with lower and upper bounds. – *Polit. Anal.* 31: 519–536.
- Kubisch, A., Degen, T., Hovestadt, T. and Poethke, H. J. 2013. Predicting range shifts under global change: the balance between local adaptation and dispersal. – *Ecography* 36: 873–882.
- Lens, F., Davin, N., Smets, E. and del Arco, M. 2013. Insular woodiness on the Canary Islands: a remarkable case of convergent evolution. – *Int. J. Plant Sci.* 174: 992–1013.
- Lenzner, B., Latombe, G., Capinha, C., Bellard, C., Courchamp, F., Digne, C., Dullinger, S., Golivets, M., Irl, S. D. H., Kühn, I., Leung, B., Liu, C., Moser, D., Roura-Pascual, N., Seebens, H., Turbelin, A., Weigelt, P. and Essl, F. 2020. What will the

- future bring for biological invasions on islands? an expert-based assessment. – *Front. Ecol. Evol.* 8: 280.
- Liu, C., Wolter, C., Xian, W. and Jeschke, J. M. 2020. Most invasive species largely conserve their climatic niche. – *Proc. Natl. Acad. Sci.* 117: 23643–23651.
- Lomolino, M. V., van der Geer, A. A., Lyras, G. A. Palombo, M. R. Sax, D. F. and Rozzi, R. 2013. Of mice and mammoths: generality and antiquity of the island rule. – *J. Biogeogr.* 40: 1427–1439. <https://doi.org/10.1111/jbi.12096>
- Lovell, R. S. L., Blackburn, T. M., Dyer, E. E. and Pigot, A. L. 2021. Environmental resistance predicts the spread of alien species. – *Nat. Ecol. Evol.* 5: 322–329.
- L  decke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P. and Makowski, D. 2021. Performance: an R package for assessment, comparison and testing of statistical models. – *J. Open Source Softw.* 6: 3139.
- Maitner, B. S., Park, D. S., Enquist, B. J. and Dlugosch, K. M. 2022. Where we've been and where we're going: the importance of source communities in predicting establishment success from phylogenetic relationships. – *Ecography* 2022: e05406.
- Mart  n-Hernanz, S., Nogales, M., Valente, L., Fern  ndez-Mazuecos, M., Pomeda-Guti  rrez, F., Cano, E., Marrero, P., Olesen, J. M., Heleno, R. and Vargas, P. 2023. Time-calibrated phylogenies reveal Mediterranean and pre-Mediterranean origin of the thermophilous vegetation of the Canary Islands. – *Ann. Bot.* 131: 667–684.
- Marx, H. E., Giblin, D. E., Dunwiddie, P. W. and Tank, D. C. 2016. Deconstructing Darwin's naturalization conundrum in the San Juan Islands using community phylogenetics and functional traits. – *Divers. Distrib.* 22: 318–331.
- Marzol, M. V. 2008. Temporal characteristics and fog water collection during summer in Tenerife (Canary Islands, Spain). – *Atmospheric Res.* 87: 352–361.
- McDougall, K. L., Lembrechts, J., Rew, L. J., Haider, S., Cavieres, L. A., Kueffer, C., Milbau, A., Naylor, B. J., Nu  ez, M. A., Pauchard, A., Seipel, T., Speziale, K. L., Wright, G. T. and Alexander, J. M. 2018. Running off the road: roadside non-native plants invading mountain vegetation. – *Biol. Invasions* 20: 3461–3473.
- M  dail, F. and Qu  zel, P. 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. – *Ann. Mo. Bot. Gard.* 84: 112–127.
- Morente-L  pez, J., Arjona, Y., Salas-Pascual, M., Reyes-Betancort, J. A., Del Arco-Aguilar, M. J., Emerson, B. C., Garc  a-Gallo, A., Jay-Garc  a, L. S., Naranjo-Cigala, A. and Pati  o, J. 2023. Biogeographic origins and drivers of alien plant invasions in the Canary Islands. – *J. Biogeogr.* 50: 576–590.
- Mucina, L. 2019. Biome: evolution of a crucial ecological and biogeographical concept. – *New Phytol.* 222: 97–114.
- Naimi, B., Capinha, C., Ribeiro, J., Rahbek, C., Strubbe, D., Reino, L. and Ara  jo, M. B. 2022. Potential for invasion of traded birds under climate and land-cover change. – *Global Change Biol.* 28: 5654–5666.
- Orihuela-Rivero, R., Morente-L  pez, J., Reyes-Betancort, J. A., Schaefer, H., Valido, A., Menezes De Sequeira, M., Romeiras, M. M., G  is-Marques, C. A., Salas-Pascual, M., Vanderpoorten, A., Fern  ndez-Palacios, J. M. and Pati  o, J. 2025. Geographic and biological drivers shape anthropogenic extinctions in the Macaronesian vascular flora. – *Global Change Biol.* 31: e70072.
- Park, D. S. and Potter, D. 2013. A test of Darwin's naturalization hypothesis in the thistle tribe shows that close relatives make bad neighbors. – *Proc. Natl. Acad. Sci.* 110: 17915–17920.
- Park, D. S. and Potter, D. 2015. A reciprocal test of Darwin's naturalization hypothesis in two Mediterranean-climate regions. – *Global Ecol. Biogeogr.* 24: 1049–1058.
- Park, D. S., Feng, X., Maitner, B. S., Ernst, K. C. and Enquist, B. J. 2020. Darwin's naturalization conundrum can be explained by spatial scale. – *Proc. Natl. Acad. Sci.* 117: 10904–10910.
- Parsons, J. J. 1983. The migration of Canary Islanders to the Americas: an unbroken current since Columbus. – *The Americas* 39: 447–481.
- Pati  o, J., Collart, F., Vanderpoorten, A., Martin-Esquivel, J. L., Naranjo-Cigala, A., Mirolo, S. and Karger, D. N. 2023. Spatial resolution impacts projected plant responses to climate change on topographically complex islands. – *Divers. Distrib.* 29: 1245–1262.
- Pearman, P. B., Guisan, A., Broennimann, O. and Randin, C. F. 2008. Niche dynamics in space and time. – *Trends Ecol. Evol.* 23: 149–158.
- Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? – *Global Ecol. Biogeogr.* 12: 361–371.
- Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C. and Guisan, A. 2012. Climatic niche shifts are rare among terrestrial plant invaders. – *Science* 335: 1344–1348.
- Pouteau, R., Giambelluca, T. W., Ah-Peng, C. and Meyer, J.-Y. 2018. Will climate change shift the lower ecotone of tropical montane cloud forests upwards on islands? – *J. Biogeogr.* 45: 1326–1333.
- POWO. 2025. Plants of the world online | kew science. – *Plants World Online*. <https://powo.science.kew.org/>
- Pulliam, H. R. and Danielson, B. J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. – *Am. Nat.* 137: S50–S66.
- Py  sek, P., Jaro   k, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U. and Vil  , M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. – *Global Change Biol.* 18: 1725–1737.
- Py  sek, P., Manceur, A. M., Alba, C., McGregor, K. F., Pergl, J.,   tajerov  , K., Chytr  , M., Danihelka, J., Kartesz, J., Klime  ov  , J., Lu  anov  , M., Moravcov  , L., Nishino, M., S  dlo, J., Suda, J., Tich  , L. and K  hn, I. 2015. Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. – *Ecology* 96: 762–774.
- Py  sek, P. et al. 2020. Scientists' warning on invasive alien species. – *Biol. Rev.* 95: 1511–1534.
- Qian, H. and Sandel, B. 2022. Darwin's preadaptation hypothesis and the phylogenetic structure of native and alien regional plant assemblages across North America. – *Global Ecol. Biogeogr.* 31: 531–545.
- Qian, H. and Sandel, B. 2023. The role of phylogenetic relatedness on success of non-native plants crossing the naturalization–invasion transition in North America. – *Ecography* 2023: e06750.
- Qian, H., Qian, S. and Sandel, B. 2022. Phylogenetic structure of alien and native species in regional plant assemblages across China: testing niche conservatism hypothesis versus niche convergence hypothesis. – *Global Ecol. Biogeogr.* 31: 1864–1876.
- Ramos-Guti  rrez, I., Lima, H., Vilela, B. and Molina-Venegas, R. 2023. A generalized framework to expand incomplete phylogenies using non-molecular phylogenetic information. – *Global Ecol. Biogeogr.* 32: 1707–1716.

- Raven, P. H., Gereau, R. E., Phillipson, P. B., Chatelain, C., Jenkins, C. N. and Ulloa Ulloa, C. 2020. The distribution of biodiversity richness in the tropics. – *Sci. Adv.* 6: eabc6228.
- Richardson, D. M. and Pyšek, P. 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. – *New Phytol.* 196: 383–396.
- Richardson, D. M. and Thuiller, W. 2007. Home away from home — objective mapping of high-risk source areas for plant introductions. – *Divers. Distrib.* 13: 299–312.
- Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D. and West, C. J. 2000. Naturalization and invasion of alien plants: concepts and definitions. – *Divers. Distrib.* 6: 93–107.
- Riera, M., Vilà, M., Melero, Y., Sáez, L. and Pino, J. 2025. Climatic niche conservatism in non-native plants is largely dependent on their climatic niche breadth in the native range. – *J. Ecol.* 113: 2301–2313.
- Robeck, P., Essl, F., van Kleunen, M., Pyšek, P., Pergl, J., Weigelt, P. and Mesgaran, M. B. 2024. Invading plants remain undetected in a lag phase while they explore suitable climates. – *Nat. Ecol. Evol.* 8: 477–488.
- Sax, D. F. and Gaines, S. D. 2008. Species invasions and extinction: the future of native biodiversity on islands. – *Proc. Natl. Acad. Sci.* 105 (Suppl. 1): 11490–11497.
- Sax, D. F., Stachowicz, J. J., Brown, J. H., Bruno, J. F., Dawson, M. N., Gaines, S. D., Grosberg, R. K., Hastings, A., Holt, R. D., Mayfield, M. M., O'Connor, M. I. and Rice, W. R. 2007. Ecological and evolutionary insights from species invasions. – *Trends Ecol. Evol.* 22: 465–471.
- Seebens, H. et al. 2017. No saturation in the accumulation of alien species worldwide. – *Nat. Commun.* 8: 14435.
- Silvertown, J. 2004. The ghost of competition past in the phylogeny of island endemic plants. – *J. Ecol.* 92: 168–173.
- Simberloff, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? – *Pac. Sci.* 49: 87–97.
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E. and Vilà, M. 2013. Impacts of biological invasions: what's what and the way forward. – *Trends Ecol. Evol.* 28: 58–66.
- Smith, S. A. and Brown, J. W. 2018. Constructing a broadly inclusive seed plant phylogeny. – *Am. J. Bot.* 105: 302–314.
- Sperling, F. N., Washington, R. and Whittaker, R. J. 2004. Future climate change of the subtropical North Atlantic: implications for the cloud forests of Tenerife. – *Clim. Change* 65: 103–123.
- Steen, B., Adde, A., Schlaepfer, M. A., Guisan, A. and Maiorano, L. 2024. Distributions of non-native and native plants are not determined by the same environmental factors. – *Ecol. Solut. Evid.* 5: e12374.
- Strauss, S. Y., Webb, C. O. and Salamin, N. 2006. Exotic taxa less related to native species are more invasive. – *Proc. Natl. Acad. Sci.* 103: 5841–5845.
- Stroud, J. T. 2021. Island species experience higher niche expansion and lower niche conservatism during invasion. – *Proc. Natl. Acad. Sci.* 118: e2018949118.
- Strubbe, D., Beauchard, O. and Matthysen, E. 2015. Niche conservatism among non-native vertebrates in Europe and North America. – *Ecography* 38: 321–329.
- Thuiller, W., Richardson, D. M., Pyšek, P., Midgley, G. F., Hughes, G. O. and Rouget, M. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. – *Global Change Biol.* 11: 2234–2250.
- Thuiller, W., Gallien, L., Boulangéat, I., De Bello, F., Münkemüller, T., Roquet, C. and Lavergne, S. 2010. Resolving Darwin's naturalization conundrum: a quest for evidence. – *Divers. Distrib.* 16: 461–475.
- Tingley, R., Vallinoto, M., Sequeira, F. and Kearney, M. R. 2014. Realized niche shift during a global biological invasion. – *Proc. Natl. Acad. Sci.* 111: 10233–10238.
- Van Kleunen, M. et al. 2015. Global exchange and accumulation of non-native plants. – *Nature* 525: 100–103.
- Van Kleunen, M., Bossdorf, O. and Dawson, W. 2018. The ecology and evolution of alien plants. – *Annu. Rev. Ecol. Evol. Syst.* 49: 25–47.
- Wallingford, P. D., Morelli, T. L., Allen, J. M., Beauury, E. M., Blumenthal, D. M., Bradley, B. A., Dukes, J. S., Early, R., Fusco, E. J., Goldberg, D. E., Ibáñez, I., Laginhas, B. B., Vilà, M. and Sorte, C. J. B. 2020. Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. – *Nat. Clim. Change* 10: 398–405.
- Whittaker, R. J., Fernández-Palacios, J. M. and Matthews, T. J. 2023. Island biogeography: geo-environmental dynamics, ecology, evolution, human impact, and conservation. – Oxford Univ. Press.
- Wiens, J. J. and Graham, C. H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. – *Annu. Rev. Ecol. Evol. Syst.* 36: 519–539.
- Wiens, J. J., Litvinenko, Y., Harris, L. and Jezkova, T. 2019. Rapid niche shifts in introduced species can be a million times faster than changes among native species and ten times faster than climate change. – *J. Biogeogr.* 46: 2115–2125.
- Wilson, J. R. U., Richardson, D. M., Rouget, M., Procheş, Ş., Amis, M. A., Henderson, L. and Thuiller, W. 2007. Residence time and potential range: crucial considerations in modelling plant invasions. – *Divers. Distrib.* 13: 11–22.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. – *Ecology* 70: 164–168.
- Yang, Q. et al. 2021. The global loss of floristic uniqueness. – *Nat. Commun.* 12: 7290.
- Yin, X., Jarvie, S., Guo, W.-Y., Deng, T., Mao, L., Zhang, M., Chu, C., Qian, H., Svenning, J.-C. and He, F. 2021. Niche overlap and divergence times support niche conservatism in eastern Asia–eastern North America disjunct plants. – *Global Ecol. Biogeogr.* 30: 1990–2003.
- Zeileis, A. and Hothorn, T. 2002. Diagnostic checking in regression relationships. – *R News* 2: 7–10.
- Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V. and Antonelli, A. 2019. Coordinatecleaner: standardized cleaning of occurrence records from biological collection databases. – *Methods Ecol. Evol.* 10: 744–751.