Moving beyond environmental filtering hypotheses – deciphering the drivers of congeneric plant introductions in an oceanic archipelago

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Abstract

Understanding why some species succeed in naturalizing and invading ecosystems, while others do not, has intrigued scientists since Darwin's time. The Pre-Adaptation Hypothesis posits that introduced species closely related to natives, and thus ecologically similar, are more likely to establish. This concept aligns with the Climate Matching Hypothesis, which emphasizes environmental similarity between native and invaded regions as a key factor in invasion success. However, conflicting evidence leaves the role of biogeographic origin and climatic affinity in predicting invasion risk unresolved. Here, we examine how biogeographical origin, climatic matching, and inter- and intraspecific pre-adaptation influence the success of congeneric plant species introduced to the Canary Islands, an oceanic archipelago with Mediterranean climatic affinities. We integrated phylogenetic, climatic and occurrence data at two levels: (i) interspecific comparisons of phylogenetic distances and climatic similarity between each introduced species and its closest native counterpart; and (ii) intraspecific analysis of climatic niche dynamics between native and introduced ranges. Most introduced congeneric species originate from the Mediterranean Basin and temperate Europe, with a notable contribution from the Neotropics. While Mediterranean and temperate European introduced taxa were phylogenetically closer to native Canarian species, we found no consistent evidence of pre-adaptation when climatic similarity among congeneric species pairs was also considered. In contrast, intraspecific analyses revealed widespread niche expansion, regardless of origin. However, species from the Mediterranean and Neotropical origin displayed a greater effect on climatic niche stability, suggesting stronger climatic matching. Overall, our findings highlight the prevalence of niche shifts among introduced plant species and underscore the role of climatic niche expansion in facilitating biological invasions. These results have key implications for assessing invasion risks in increasingly disturbed insular regions worldwide.

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origin and climatic affinity in predicting invasion risk unresolved. Here, we examine how biogeographical origin, climatic matching, and pre-adaptation influence the success of congeneric plant species introduced to the Canary Islands, an oceanic archipelago with Mediterranean climatic affinities. We integrated phylogenetic, climatic and occurrence data at two levels: (i) interspecific comparisons of phylogenetic distances and climatic similarity between each introduced species and its closest native counterpart; and (ii) intraspecific analysis of climatic niche dynamics between native and introduced ranges. Most introduced congeneric species originate from the Mediterranean Basin and temperate Europe, with a notable contribution from the Neotropics. While Mediterranean and temperate European introduced species were phylogenetically closer to native Canarian species, we found no consistent evidence of pre-adaptation when climatic similarity among congeneric species pairs was also considered. In contrast, intraspecific analyses revealed widespread niche expansion, regardless of origin. However, species from the Mediterranean and Neotropical origin displayed a greater effect on climatic niche stability, suggesting stronger climatic matching. Overall, our findings highlight the prevalence of niche shifts among introduced plant species and underscore the role of climatic niche expansion in facilitating biological invasions. These results have key implications for assessing invasion risks in increasingly disturbed insular regions worldwide.

Keywords

biological invasions; biogeographic regions; Canary Islands; climatic niche dynamics; climate matching; phylogenetic relatedness

Introduction

Biological invasions are major drivers of global change, posing significant threats to human health, economies, and biodiversity (Cronk and Fuller 2013, Pyšek 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 have however received comparatively less attention in the empirical 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 the climate resembles that 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 Pysek 2012, Enders et al. 2020). At its core, CMH assumes that introduced species succeed when they encounter environments analogous to those they are evolutionarily adapted to; an idea sometimes linked to the notion of "*pre-*

adaptation ". However, to avoid confusion with DPAH, we refrain from using that term here. Recent advances in niche theory provide a valuable lens through which to assess whether introduced species remain constrained within their original climatic niches. This perspective allows us to test fundamental evolutionary processes, particularly intraspecific niche conservatism, and evaluate their role in shaping patterns of biological invasion (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 expansion (e.g. Petitpierre et al. 2012, Liu et al. 2020). Conversely, substantial evidence also points to niche shifts and expansions following naturalization (e.g. 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). These authors 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).

In the context of biological invasions, oceanic islands rank among the most vulnerable ecological systems (Donlan et al. 2003, Sax and Gaines 2008, Pyšek et al. 2012, Carine and Menezes de Sequeira 2020). Their susceptibility to human-mediated naturalization stems from unique features such as a volcanic origin and a consistent geographic isolation, which create systems with limited resilience to biological invasions (e.g. Simberloff 1995, Caujapé-Castells et al. 2010, Dawson et al. 2017, Lenzner et al. 2020). The Canary Islands provide an intriguing case study for investigating the processes driving biological invasions. While both the climate and the native Canarian flora are predominantly Mediterranean in origin (Carine et al. 2010, del Arco-Aguilar and Rodríguez-Delgado 2018), the primary biogeographic origin of invasive introduced plants is the Neotropics, which outnumber contributions from other regions with Mediterranean-type climates (Morente-López et al. 2023).

The pattern observed in the Canary Islands can be attributed to several non-exclusive factors. First, the Neotropical region possesses much higher levels of diversity than other regions (Raven et al. 2020). Second, historical patterns of human migration between the Canary Islands and the Americas have consistently promoted species exchange (Parsons 1983). Third, the lower number of Mediterranean and European introduced species may partly reflect the misclassification of introduced species as native (Carlton 1996, Morente-López et al. 2023). While this pattern may initially appear to challenge both the CMH and the DPAH, further studies focusing on the climatic niches occupied by introduced species in the Canarian archipelago are essential to either validate or refute these hypotheses.

Following an integrative approach (Fig. 1), we compiled biogeographic, phylogenetic, and occurrence data for both native and introduced plant species in the Canary Islands. Using this dataset, we calculated climatic envelopes (i.e. the climatic component of the ecological niche or the "*climatic niche* ", Pearson and Dawson 2003) and phylogenetic distances to test the two hypotheses referred: the DPAH through interspecific comparisons, and the CMH, via intraspecific comparisons. To minimize potential biases, particularly the overrepresentation of Neotropical species and underrepresentation of Mediterranean taxa, we restricted our analysis to extant genera containing both native and introduced species (see Steen et al. 2024). Focusing on congeneric species, which often share functional traits and evolutionary histories (e.g. Yin et al. 2021), provides a robust framework for identifying features that confer either invasiveness or resistance to invasion (Daehler 2001, Strauss et al. 2006).

Specifically, we address the following questions: (i) From which climate types and biogeographic regions do introduced congeneric plant species originate from? (ii) Is there a relationship between phylogenetic relatedness and climatic similarity between native and introduced congeners, suggesting interspecific phylogenetic niche conservatism as a driver of invasion success? (iii) Do niche dynamics between the native and introduced ranges point to intraspecific niche conservatism as a central mechanism during species naturalization?

(iv) To what extent do climatic pre-adaptation (*sensu* Darwin) and niche dynamics vary depending on the biogeographic origin? Building on previous findings that biodiversity hotspots with Mediterranean-type climates frequently receive introductions from climatically similar regions (Casado et al. 2018, Cao Pinna et al. 2021), we hypothesize that closely related introduced species will mostly originate from the Mediterranean Basin and will exhibit high climatic similarity with their native congeners and ranges, reflecting strong inter- and intraspecific niche conservatism. Species arriving from other Mediterranean-type climates are expected to display comparable patterns, though potentially with lower interspecific niche conservatism due to different evolutionary histories. In contrast, more distantly related species, particularly those from non-Mediterranean-type regions (e.g. Neotropics), are expected to occupy less similar climatic niches, indicating lower levels of both inter- and intraspecific climatic niche conservatism.

Materials and methods

Study area

The Canary Islands, an oceanic archipelago located in the northeast Atlantic Ocean, form part of the Macaronesian biogeographic region (Fernández-Palacios et al. 2024). Characterized by a subtropical Mediterranean climate (del Arco-Aguilar and Rodríguez-Delgado 2018), the archipelago is a well-established model for studying biodiversity patterns and the underlying ecological and evolutionary mechanisms (Florencio et al. 2021). These islands represent a westward extension of the Mediterranean Basin Hotspot into the Atlantic Ocean (Médail and Quézel 1997), and are recognized for their exceptional levels of endemicity, with around 40% of the native vascular flora being endemic (del Arco-Aguilar and Rodríguez-Delgado 2018). The region also harbors around 900 introduced species, comprising *ca* . 32% of the total flora (Gobierno de Canarias 2025). Our study focused on all seed plant genera that include both native and introduced species in the archipelago. This dataset includes 97 genera and 631 congeneric species, accounting for 30% of the introduced flora (Gobierno de Canarias 2025, Supporting Information S1.1).

Origin and biogeographical classifications

Each species was assigned its native or introduced status based on the BIOTA platform (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, 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 congeneric species in the Canary Islands, 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) (Fig. 2A). 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 S1.2). 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, temperate Europe, and the Neotropical regions.

Occurrence data

Out of the 97 genera containing both native and introduced congeneric species, fifteen were excluded altogether due to insufficient occurrence data for some or all species in the archipelago, or because neither native and/or introduced species were represented in our backbone phylogeny (Supporting Information S1.1). The remaining 82 genera (84.5% of the total) were retained for interspecific comparisons, encompassing 182 introduced species (67.4% of all introduced congeneric species). For intraspecific comparisons between native and invaded ranges, an additional 62 species were removed due to insufficient occurrence data in the invaded range. Consequently, this analysis included 65 congeneric genera (67.0% of the total), covering 65 genera and 120 introduced species (44.6% of all introduced congeneric species).

We gathered species occurrence data from 1970 to the present. For the Canary Islands, distribution data were retrieved from the Biodiversity Data Bank of the Canary Islands (BIOTA, Gobierno de Canarias 2023). For the native ranges of introduced species and the non-Canarian ranges of native species, we used GBIF (GBIF, 2023, Supporting Information S1.1). Concerning data in the BIOTA database, we only retrieved records at the first two levels of resolution, using centroids of each 500 m x 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, 8,887,056 raw GBIF occurrences were reduced to 1,878,496 records. BIOTA data, already filtered, provided an additional 359,036 occurrences.

Climatic data

For climatic data, we used the 19 bioclimatic variables obtained from two different climate datasets. For the non-Canarian range, we extracted present-day variables from CHELSA v2.0 (Karger et al. 2017, 2021) at a 30 arc-second resolution (~1 km). For the Canary Islands range, we utilized the CanaryClim v1.0 dataset (Patiño et al. 2023), a downscaled version of CHELSA tailored for the archipelago. To ensure consistency with the BIOTA species occurrence data, all climatic layers were resampled to a 500 × 500 m grid.

Phylogenetic distance inference

We constructed species-level backbone phylogenetic trees for each of the 82 genera considered in the present study (Supporting Information S1.1). We used the 'V.PhyloMaker2' R package (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) 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 Supporting Information S1.3. 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

To assess the similarity of climatic niches between congeneric native and introduced species, we first compared species pairs of native and introduced species (as done through models in Steen et al. 2024). Niche overlap was evaluated in environmental space using Schoener's D values (Broennimann et al. 2012), which quantifies climate niche similarity while accounting for differences in the environmental conditions across their background space (Guisan et al. 2014). Differences in Schoener's D indicate distinct environmental preferences that are not merely a consequence of available geographic conditions (Broennimann et al. 2012).

We computed climatic niche similarity using the 'ecospat' R package (di Cola et al. 2017), which estimates species' climatic niches through Environmental Principal Component Analysis (PCA-env). The degree of overlap between these PCA-envs quantifies the degree of niche overlap in the environmental space (Graham et al. 2004). Kernel Density Estimation (Worton 1989) was further applied to the occurrence densities in PCA-env space to produce smooth, continuous representations of realized climatic niches, minimizing artifacts related to grid resolution (Broennimann et al. 2012, Guisan et al. 2012).

To tackle niche dynamics of the introduced species at the intraspecific level, we also generated climatic envelopes for each of the 120 for each introduced species selected using the 'ecospat' R package (di Cola et al. 2017). Following Guisan et al. (2014), we calculated three niche metrics: (i) expansion, the proportion of the invaded range that falls outside the climatic conditions of the native range; (ii), stability, the proportion of overlapping climatic niches between the native and invaded ranges; and (iii) unfilling, the proportion of the native range's climatic conditions that are not occupied in the invaded range.

Statistical analyses

To test our two main hypotheses (Fig. 1), namely DPAH and CMH, we relied on a generalized linear mixed modelling approach (GLMM) as follows. DPAH was evaluated using interspecific comparisons of the relationship between climatic similarity and phylogenetic distance, while CMH focused on intraspecific comparisons of niche dynamics, namely on the metrics of expansion and stability. We did not consider unfilling, as this metric mainly reflects properties of species' native ranges rather than invasion dynamics within the invaded range.

More specifically, we assessed whether phylogenetic distance influenced climatic similarity between native and introduced congeneric species. Climatic similarity (measured as Schoener's D) was the response variable, modeled using an ordered beta distribution, appropriate for bounded proportion data (Kubinec 2023). Phylogenetic distance was included as the predictor variable, with genus as a random factor to account for the hierarchical structure (i.e. multiple species pairs within genera). GLMMs were implemented using the 'glmmTMB' R package (Brooks et al. 2017), and model diagnostics (normality and homoscedasticity of residuals) were evaluated with the 'DHARMa' R package (Barreto et al. 2021, Hartig, 2023). We also fitted a null model, including only the random factor, to assess if the added value of incorporating the phylogenetic distance significantly improved the models' fits beyond the variation explained by genus alone. Model selection was performed using the corrected Akaike's information criterion for small samples (AICc) from the 'bblme' R package (Bolker 2022). Models were ranked based on ΔAICc, with models having a ΔAICc [?] 2 relative to the best model considered to have substantial support (Burnham and Anderson, 2002). GLMMs were conducted on the full dataset and separately for each of the four biogeographic subsets (i.e. Mediterranean Basin, other Mediterranean-type regions, temperate Europe, and Neotropics). We also repeated the analyses with a reduced dataset excluding UPS to ensure the robustness and rule out potential bias from incorrectly assigned UPS.

Second, to test CMH, we modeled expansion and stability metrics as response variables, again using ordered beta distributions. Predictor variables included the presence/absence of native status in each of the four biogeographic regions (Mediterranean Basin, temperate Europe, Neotropics, other Mediterranean-type regions) and invasion stage (naturalized or invasive). Genus was included as a random factor. We applied the 'MuMIn' R package (Barton, 2022) to construct all possible combinations of predictor variables and selected the most supported models based on the ΔAICc threshold already described (Burnham and Anderson, 2002). Diagnostic checks were again conducted using the 'DHARMa' R package. To disentangle the relative influence of geographic 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) provided 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 (see Methods), we provide a general overview of the climatic and biogeographic affinities of all introduced species. Most introduced taxa originated from temperate (54.5%) and subtropical (27.9%) climatic zones, with smaller proportions from dry (10.1%), wet tropical (3.7%), and desert climatic zones (3.7%) (Fig. 2B, Supporting Information S1.2). 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. 2A). 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. 2C, Supporting Information S1.2).

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 (Supporting Information S1.3). Among these, 31 were assigned as sister species or singletons, while 103 were placed within the most derived consensus clades supported by prior studies.

Phylogenetic distances between introduced and native congeners varied by biogeographic region. 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 $p < 0.05$, Supporting Information Fig. S2.2). In contrast, Neotropical congeners showed significantly greater phylogenetic distances to their native counterparts compared to species from other regions ($p < 0.05$, Supporting Information Fig. S2.2). No significant differences were observed for species originating from other Mediterranean-type climate regions ($p > 0.05$).

Climate similarity at the interspecific level

Overall, climatic similarity between introduced species and their nearest native congeners was low, regardless of biogeographic origin (Supporting Information S1.4). Models testing for pre-adaptation, specifically those including phylogenetic distance as a predictor of climatic similarity, received no statistical support. Across all analyses, the null model consistently ranked as the best or among the best-fitting models, both for the full dataset and for subsets grouped by the biogeographic origin of introduced species, with the only exception of the full model where the model including phylogenetic distance was also included among the best fitting models (ΔAICc = 1.8, Table 1). These results remained robust when using those datasets where UPS were not considered (Supporting Information S1.5).

Climatic niche dynamics at the intraspecific level

Climatic niche expansion was extensive among the introduced species examined, although there was considerable variability across taxa. Across the full dataset, the metrics expansion and unfilling exhibited high mean values (0.71 ± 0.37 and 0.86 ± 0.25, respectively), whereas stability consistently showed the lowest values (0.21 ± 0.32, Supporting Information S2.1). Among biogeographic regions, species from the Mediterranean Basin and temperate Europe exhibited the highest average expansion (0.73 ± 0.36 and 0.75 ± 0.37, respectively) and the lowest stability (0.19 ± 0.31 and 0.12 ± 0.24). In contrast, species from the Neotropics had lower expansion (0.55 ± 0.43) and unfilling (0.77 ± 0.35), and comparatively higher stability (0.36 ± 0.41, Supporting Information S2.1).

Out of the 120 introduced species included in the niche dynamic analyses, 41 (34%) exhibited complete niche expansion (i.e. expansion = 1), while 77 (64%) showed expansion values [?] 0.75. Complete expansion was most frequent among species from temperate Europe (40%) and the Mediterranean Basin (35%). The Neotropics had the lowest proportion of species with complete expansion (24%), although 52% still had values [?] 0.75. Among species from other Mediterranean-type regions, 29% showed complete expansion and 62% had values [?] 0.75 (Supporting Information S1.6).

Model selection based on ΔAICc identified eight top-ranking models for expansion and five for stability out of 33 possible predictor combinations (Supporting Information S1.7). Averaged models retained biogeographic origin and invasion stage as relevant predictors, although their influence varied. The Neotropics and Mediterranean Basin had the highest summed weights for both expansion (sw = 1 and sw = 0.61, respectively) and stability (sw = 1 for both, Fig. 3). In contrast, predictors such as temperate Europe, other Mediterranean-type regions, and invasion stage had lower weights (sw $<$ 0.55). Standardised coefficients revealed that expansion was negatively associated with native presence in the Neotropics and, to a lesser extent, in the Mediterranean Basin. Conversely, stability was positively correlated with native presence in both the Neotropics and Mediterranean Basin (Supporting Information S1.8).

Discussion

By integrating phylogenetic relationships with distribution data from both native and introduced congeneric species, we independently tested both ‘ Darwin’s pre-adaptation hypothesis’ (DPAH) and the‘ Climate matching hypothesis’ (CMH). Interspecific comparisons between congeneric species did not consistently support the DPAH. 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

The introduced congeneric flora of the Canary Islands originates predominantly from temperate and subtropical climate zones, particularly the Mediterranean Basin and temperate Europe. This aligns with two key patterns: (i) 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 (ii) the Mediterranean Basin as a key donor to other regions with a Mediterranean-type climate (Kalusová et al. 2017, Casado et al. 2018, Cao Pinna et al. 2021). Long-standing human-plant interactions in Mediterranean and European landscapes likely facilitated species adaptation to anthropogenic environments, increasing invasion potential (Di Castri 1989, Jeschke and Strayer 2005, Hierro et al. 2006, Kalusová et al. 2017, McDougall et al. 2018). However, these trends are specific to congeneric species and may not extend to the entire naturalized and invasive flora of the Canary Islands (Morente-López et al. 2023). Understanding the drivers behind these patterns remains a key challenge but also an opportunity to refine predictions about invasion dynamics (Pyšek et al. 2015, van Kleunen et al. 2018, Gioria et al. 2023).

Limited climatic support for Darwin´s Pre-adaptation hypothesis

Although Mediterranean and temperate European introduced congeneric species are phylogenetically closer to native Canarian species, supporting patterns evidenced during the assembly of the native vascular flora (Carine et al. 2010, Martín-Hernanz et al. 2023, reviewed in Fernández-Palacios et al. 2024), we found no relationship between phylogenetic distance and climatic similarity. This pattern holds across all biogeographic origins and under reduced-dataset analyses without UPS. Such findings challenge the DPAH and therefore the idea that climatic niche conservatism across clades of closely related species is a general mechanism promoting invasion success (Park et al. 2020, Quian and Sandel 2022).

These results contrast with broader-scale studies that link pre-adaptation with invasion success (Park and Potter 2015, Park et al. 2020, Quian 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 consistent relationships with climatic similarity by leading to increased, clustering, or neither dispersion (Cadotte et al. 2009, Quian and Sandel 2022, 2023). Spatial niche truncation due to sampling limitations or restricted climatic ranges may also mask potential patterns (Guisan et al. 2014, Chevallier et al. 2021). Complementing DPAH, *‘Darwin’s Naturalization hypothesis’* predicts the success of introduced species that are distantly related to the native species of the occupied natural ecosystem (Díez et al. 2008). While our results could point towards this last hypothesis, the rationale behind it cannot be validated from our methodology. Regardless, these findings emphasize the complementary role to interspecific approaches of intraspecific climatic dynamics when testing invasion hypotheses such as DPAH (Haubrock et al. 2024).

On the dynamics of climatic niches

Climatic niche expansion was prevalent among the introduced species studied, while niche stability remained low overall. Indeed, over a third (34%) of species exhibited complete climatic niche expansion, and another 30% showed an expansion metric value of at least 0.75. Across all biogeographic origins, stability consistently exhibited the lowest mean values, while expansion and unfilling were comparatively higher. Under this general framework, model selection identified several predictors of niche expansion and stability. The Mediterranean Basin and the Neotropics had the greatest weight in top-ranked models, with a significant positive effect on climatic niche stability. Conversely, being native to the Neotropics was negatively associated with niche expansion, with only marginal effects for the Mediterranean Basin.

These patterns likely reflect the heterogeneous climatic gradients, both altitudinally and longitudinally, of the Canary Islands, driven by sharp topographic gradients and the proximity to Africa (del Arco-Aguilar and Rodríguez-Delgado 2018, Patiño et al. 2023), which resemble those of both Mediterranean and Neotropical semi-arid regions. Climatic similarities, reflected in the positive effect of the metric stability, likely facilitated naturalization and spread, particularly among xerophytic species adapted to seasonally dryness through diverse strategies (e.g. Gianoli and Molina-Montenegro, 2021, Ferreras et al. 2023). However, attributing invasion success solely to climatic matching and partial support for the CMH oversimplifies the underlying processes. Notably, the relatively weak effect of the invasion stage on climatic niche dynamics suggests a potential misclassification of species as naturalized or invasive (Patiño et al. 2015, Morente-López et al. 2023). Targeted reassessment of species such as *Crassula ovata* and*Solanum laxum* may help clarify their true invasion potential.

Understanding niche shifts beyond climate matching

Although in a limited fashion following our modelling approach, our findings reinforce former evidence that niche expansion is common in biological invasions (but see Petitpierre et al. 2012, Liu et al. 2020), with or without fundamental niche modifications (Broennimann et al. 2007, 2014, Tingley et al. 2014, Guisan 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). This overwhelming signature of climatic niche expansion may be driven by ecological release from natural or anthropogenic biotic constraints (e.g. interspecific competition, predation) or dispersal limitations in the native range (Catford et al. 2011, van Kleunen et al. 2018, Gioria et al. 2023). The disharmonic and less competitive ecosystems of oceanic islands like the Canary Islands may have further facilitated niche expansion (Silvertown 2004, König et al. 2021).

Alternatively, niche shifts may be driven by *in situ* rapid evolution, leading to changes in species' fundamental niche tolerances (Kubish et al. 2013, Wiens et al. 2019). Besides this, climatic mismatch can also reflect spread lags, where introduced species have yet to occupy their full potential climatic space (Petitpierre et al. 2012). In other words, a lag between colonization and full range expansion can take place, derived from for instance their residence time (Wilson et al. 2007, Gioria et al. 2023), among other intrinsic and extrinsic factors (Robeck et al. 2024). This phenomenon, known as "*invasion debt* " (Essl et al. 2011, Cao Pinna et al. 2024), is supported in our study by high levels of niche unfilling. These lags further complicate our ability to predict future spread and invasion events (Sax et al. 2007) and highlights the need for ongoing monitoring and integrative early-detection approaches, including mapping and scanning exercises (Simberloff et al. 2013, Hulme 2025).

Overall, our results indicate that many introduced species remain far from climatic equilibrium in their invaded ranges. This disequilibrium underscores the potential for continued range expansion under changing climatic and environmental scenarios (Wallingford et al. 2020, Naimi et al. 2022, Gioria et al. 2023). Given that our estimates of niche dynamics are based on a limited temporal and spatial window (i.e. reflecting both occurrence and climate data spanning only a few decades, Atwater et al. 2018), future research should adopt broader temporal and geographic scales, incorporate more comprehensive phylogenetic frameworks, and integrate non-climatic predictors to better capture the complexity of plant invasion dynamics and niche shifts at both inter- and intraspecific levels (Cadotte et al. 2018, Lovell et al. 2021, Maitner et al 2022).

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Figure Captions

Figure 1

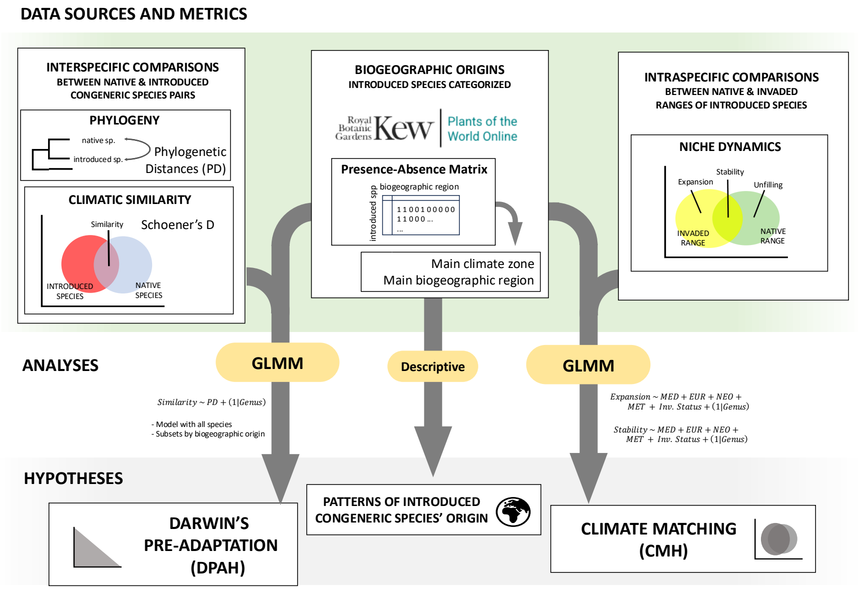
Methodological concept map illustrating the workflow used to assess the roles of biogeography, climate and phylogeny in the success of introduced congeneric species in the Canary Islands. The diagram outlines the data sources, metrics, analyses and how these were used to test *'Darwin's pre-adaptation'* (DAPH) and the *'Climate Matching'* (CMH) Hypotheses separately. Specifically, we describe the three key types of data: (i) biogeographic origins of the introduced species (central position) were retrieved from Plants of the World Online (POWO, 2024) to generate a matrix of the distribution of species across different biogeographic regions, namely the Mediterranean Basin (MED), temperate Europe (EUR), other Mediterranean-type regions (MET) and the Neotropics (NEO); (ii) interspecific comparisons (left position) between each introduced species and its phylogenetically nearest native congeneric species we computed through phylogenetic distances and climatic niche similarity measured through Schoener's D; and (iii) intraspecific comparisons (right position) between native and invaded ranges of exotic species through three niche dynamics metrics (Expansion, Stability and Unfilling). We described the general biogeographic patterns of introduced congeneric species, to then combine the descriptive distribution data and the generated metrics to test DPAH and CMH, respectively, through Generalized Linear Mixed Models (GLMMs) (See Materials and Methods Section for details).

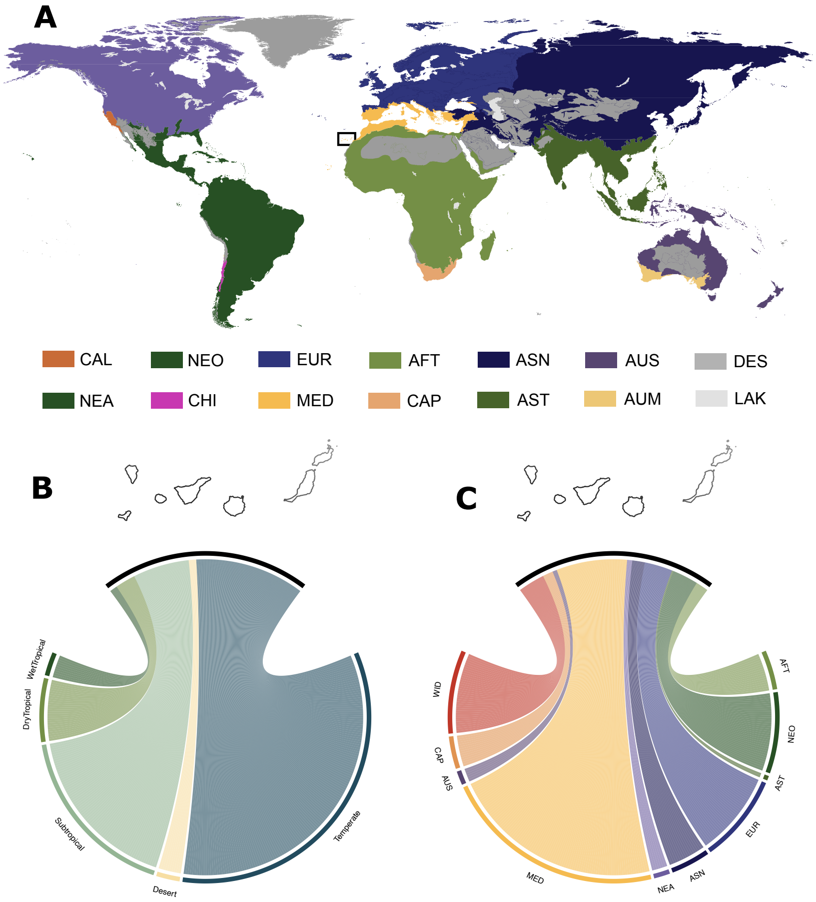
Figure 2

(A) Global biogeographical regions used in this study with the Canary Islands highlighted in the black rectangle (adapted from Morente-López et al. 2023). EUR: temperate Europe, excluding the Mediterranean Basin; AFT: tropical Africa excluding the Maghreb and Cape region; CAP: Cape floristic region; ASN: Palearctic East Asia; AST: tropical Asia; AUS: Australasia; AUM: south-western Australia; NEO: Neotropics, excluding central Chile; NEA: Nearctic, excluding the Californian Province; CHI: central Chile; CAL: California Floristic Province; DES: cold or hot (semi)deserts. **(B)** Proportion of the introduced congenerics in the Canary Islands based on their main climatic zone of origin as defined by Govaerts et al. (2021) are WetTropical: Wet tropical biomes; DryTropical: dry tropical biomes; Subtropical: subtropical biomes; Desert: desertic biomes; Temperate: temperate biomes. **(C)** Proportion of the introduced congenerics in the Canary Islands based on their main biogeographic region of origin. The main biogeographic region was selected based on the presence-absence matrix (see main text).

Figure 3

Coefficient estimates from average generalized linear mixed models (GLMMs), where **(A)** shows the relation with the expansion proportion and **(B)** the stability proportion. Coefficients left to the red line (0), represent that the presence as native of a species in that particular region or in one or the other invasion categories is correlated with lower expansion or stability values. Coefficients right to the red line indicate higher values of expansion or stability for the presence or invasion status. We also provide the sum of model weights (*sw*) for each variable and averaged model.

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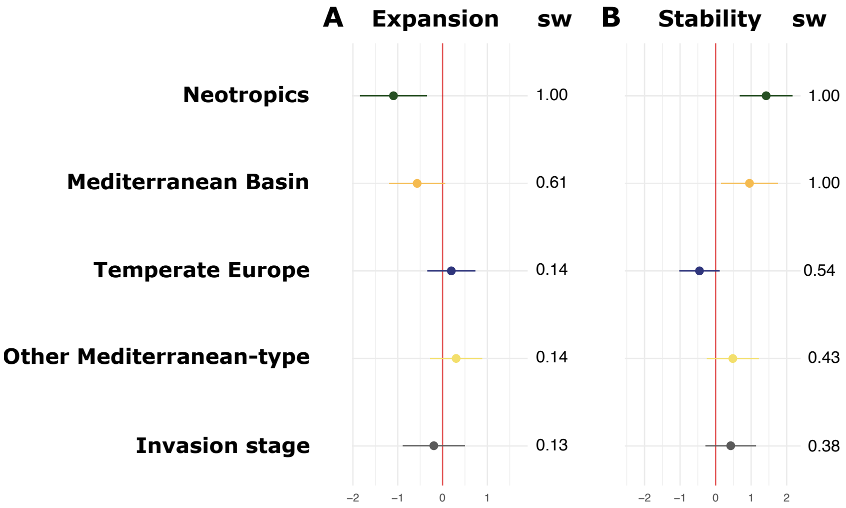
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