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RESEARCH ARTICLE

Climatic niche conservatism in non-native plants is largely dependent on their climatic niche breadth in the native range

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Abstract

1. Confidence in predictions of non-native species' spread relies on the niche conservatism hypothesis, which poses that climatic niches are preserved over time and space. Because plants introduced through the same introduction pathway (gardening, unintentional) tend to share some features of the introduction process and biological attributes, the extent of niche conservatism might be influenced by how and when species of particular attributes have been introduced.
2. We compared the realized climatic niches between the native (global) and invaded ranges (mainland Spain), through ordination and kernel smoothers. We calculated niche conservatism metrics (i.e. overlap, unfilling, stability, expansion and pioneering), for a set of 158 plant species. Niche conservatism metrics were then related to a plant's introduction pathway, minimum residence time, growth form and native climatic niche breadth.
3. On average, niche stability accounted for 75% of niche occupancy, while around 61% of species showed some degree of niche shift, which were mostly of small magnitude. The climatic niche was most conserved for annual and perennial herbs, plants introduced a long time ago, and those with broad climatic niches in their native range. Introduction pathways had a non-significant effect. Niche conservatism metrics were neither explained by interactions of minimum residence time with introduction pathways nor with growth form. Native climatic niche breadth was the most important correlate of niche conservatism metrics.
4. *Synthesis*. Non-native plants largely occupy similar climatic conditions in their invaded and native range, a pattern that co-occurred with frequent and mostly small niche shifts. These results largely support the niche conservatism hypothesis. This boosts confidence in predictive models of non-native plants' spread. This study highlights that niche conservatism is better explained by a plant's ability to cope with broad climatic conditions, rather than by its introduction history or growth form.

KEYWORDS
ecological niche modelling, growth form, introduction pathway, invasion ecology, minimum residence time, niche breadth, niche conservatism, niche dynamics, niche shifts, species distribution modelling

1 | INTRODUCTION

The ecological niche, defined as the set of environmental conditions that allow population persistence for a particular species, is a key concept in ecology and conservation biology (Guisan et al., 2014). Importantly, the niche is the theoretical basis of ecological niche models (ENMs), which predict the distribution of species by matching their occurrence to environmental conditions (Franklin, 2010; Guisan et al., 2014). The majority of ENMs approximate the realized niche through field observations, rather than the fundamental niche based on ecophysiological requirements (Guisan et al., 2014). ENMs are essential for effective conservation strategies (Guisan et al., 2014; Liu et al., 2020), including the management of invasive species, in order to prioritize resources to prevent and curb their spread in the areas identified as suitable by models (McGeoch et al., 2016). Indeed, many non-native plant species have not yet spread to occupy their potential distribution range (Gassó et al., 2010, 2012). The pervasive negative effects of invasive species (Bacher et al., 2024) highlight the need for reliable prediction of their spread (Liu et al., 2022).

An important factor that boosts the reliability of predictions of non-native species' spread is niche conservatism (Liu et al., 2022): similar occupancy of environmental conditions in the invaded range compared with the native range (Pearman et al., 2008; Peterson, 2011). Most evidence concerning niche conservatism comes from non-native plants (Liu et al., 2020). While some studies have reported substantial conservatism (Liu et al., 2020; Petitpierre et al., 2012), some have found important niche shifts between ranges (Atwater et al., 2018; Early & Sax, 2014). Therefore, substantial interest lies in understanding the factors influencing the extent of niche conservatism.

A plant's introduction pathway (the type of human activity responsible for its introduction, such as gardening or unintentional transport; Hulme et al., 2008) can influence niche conservatism (Atwater et al., 2018; Liu et al., 2020). These effects are likely related to pathway-specific differences in human husbandry and climate matching in introduction epicentres (i.e. initial points of introduction and spread; Donaldson et al., 2014). For example, cultivation has been related to reduced niche conservatism compared with unintentional introductions at the global scale (Atwater et al., 2018), possibly because human husbandry increases the chance of population establishment (Gallagher et al., 2010). However, a meta-analysis found similar niche conservatism among plants introduced only intentionally or only unintentionally, with a combination of intentional and unintentional introduction leading to greater niche conservatism (Liu et al., 2020). Overall, the scarcity of previous studies (Table S1) makes it difficult to reach a general understanding of the differences in niche conservatism among plant species introduced for gardening and those introduced unintentionally, which are main introduction pathways world-wide (Hulme et al., 2008). This is an important knowledge gap, given the crucial role of introduction pathways in the design of preventive management strategies in biological invasions (McGeoch et al., 2016).

Because introduction pathways of non-native plants have changed over time (Cerrato et al., 2023; Riera et al., 2024), we expect the effect of introduction pathways on niche conservatism to depend on minimum residence time (i.e. time since first record outside cultivation). Previous studies indicate that unintentional introductions have become partly decoupled from agricultural introductions (Cerrato et al., 2023; Riera et al., 2024; Sanz-Elorza, Mateo, & Bernardo, 2009), and are recently more closely related to trade and tourism (Ansong & Pickering, 2014; Lucardi et al., 2020). Importantly, agricultural weeds tend to experience high climate matching because they are pre-adapted to the same climate as the crops they infest, unlike introductions with trade and tourism (Neve et al., 2009; Peters et al., 2014). Therefore, increasing residence time would correlate to decreasing climate matching among unintentionally introduced plants. Previous studies on minimum residence time generally reported negative correlations with niche conservatism (Early & Sax, 2014; Liu et al., 2020), although some studies report no or a weak positive effect (Gallagher et al., 2010; Petitpierre et al., 2012; Sychrová et al., 2022). To the best of our knowledge, whether niche conservatism is influenced by an interaction between minimum residence time and introduction pathways has not been previously tested (Table S1).

Plants with a common pathway also tend to share some biological attributes: unintentionally introduced plants are more likely to be herbs (Atwater et al., 2018; Riera et al., 2024) and to have wider climatic niches in their native range, in comparison with gardening plants (Riera et al., 2024). Moreover, because herbaceous growth form and short height correlate to faster rates of molecular and niche evolution among plant lineages (Lanfear et al., 2013; Smith & Beaulieu, 2009), herbaceous non-native plants could be more likely to evolve changes in their fundamental niches than shrubs and trees. However, previous studies show more niche conservatism among herbs than among shrubs and trees (Atwater et al., 2018), no effect of growth form (Gallagher et al., 2010) or no effect of generation time (nor in interaction with minimum residence time; Early & Sax, 2014). Therefore, it remains unclear whether there is a consistent effect of growth form on niche conservatism. Likewise, plants with a wide climatic niche in the native range might have less climate space left to occupy, promoting the extent of niche conservatism (Dellinger et al., 2016; Early & Sax, 2014; Sychrová et al., 2022). It remains to be tested which is the simultaneous influence of introduction pathway, minimum residence time, growth form and climatic niche breadth in the native range on niche conservatism (Table S1).

In this study, we draw data on 158 plant species invading mainland Spain, to test whether niche conservatism is modulated by introduction pathways, growth form, native climatic niche breadth and minimum residence time; while accounting for potential interactions. Specifically, we expect: (1) reduced niche conservatism for gardening plants than for unintentionally introduced ones (Atwater et al., 2018); (2) greater niche conservatism with increasing minimum residence time, particularly for unintentionally introduced plants; (3) reduced niche conservatism in annual and perennial herbs compared with shrubs and trees, particularly for annual herbs with greater minimum residence time (Early & Sax, 2014); and finally (4) greater niche conservatism among plants with wider niches in the native range (Dellinger et al., 2016; Early & Sax, 2014).

2 | METHODS

2.1 | Plant occurrences in the native and invaded ranges

We used the non-native vascular flora of mainland Spain as a study-system because of its diverse environmental conditions: this area encompasses 12 climate types, from hot desert to subarctic (Instituto Geográfico Nacional, 2019). Furthermore, Spain has experienced temporal changes in pathway importance that allow us to test our second expectation (Riera et al., 2024; Sanz-Elorza, Mateo, & Bernardo, 2009).

We compiled a list of naturalized neophytes in mainland Spain from Sanz-Elorza et al. (2004). Naturalized neophytes are non-native plant species introduced to Spain after 1500, which form stable populations without human intervention. We harmonized the nomenclature using the Plants of the World Online website (POWO, 2021). We did not include in our analyses: aquatic and parasitic species, those without data on the year of first record, nor those introduced only through agriculture or forestry (due to small sample size), leading to a preliminary selection of 300 species.

We downloaded occurrence coordinates from the Global Biodiversity Information Facility (GBIF, 2021), using the 'rgbif' package (Chamberlain et al., 2021). We filtered the download relying on available metadata and the 'CoordinateCleaner' package (Zizka et al., 2019), with full details provided in the Supplementary methods (Feng et al., 2019).

Polygons delimiting the native range (anywhere in the world) and invaded range (in Spain) were taken from the Taxonomic Database Working Group (Brummitt, 2001), using three nested scales: level 1 (continental) > level 2 (sub-continental to sub-national) > level 3 (national to sub-national).

The native range were level 2 regions taken from the Plants of the World Online webpage (POWO, 2021). A quality-check was performed by comparing level 2 regions against Germplasm Resource Information Network (GRIN, 2021), and by comparing level 1 regions against Sanz-Elorza et al. (2004). Moreover, we kept some species considered by POWO as native to Spain, following the more updated checklist of the vascular flora of the Iberian Peninsula (Ramos-Gutiérrez et al., 2021). This led to the correction of 14% of the species in the final dataset (Table S2). The invaded range was the level 3 polygon delimiting mainland Spain.

We overlaid the filtered GBIF occurrence data, onto the polygons delimiting the native and invaded ranges ('sf' package; Pebesma, 2018). We kept plants with at least 20 occurrences in both the native and invaded ranges, reducing our initial selection from 300 to 158 species.

2.2 | Climatic niches

For each species, we calculated its realized climatic niche (hereafter, 'climatic niche'), by extracting 19 bioclimatic variables on the occurrences, at a resolution of 2.5 arc-minutes from WorldClim v1.4 (Hijmans et al., 2005), using the 'raster' package (Hijmans, 2021). We kept a single occurrence per pixel.

We used the relevant level 2 polygons for the native background climate (potentially different for each species), removing those polygons with no GBIF occurrences (2% of species; Table S3). All species had the same invaded background climate (mainland Spain).

2.3 | Climatic niche conservatism

We decomposed the climatic niche through ordination and kernel density smoothing (PCA-env; Broennimann et al., 2012), which has become a gold standard to study climatic niche conservatism (Liu et al., 2020). This approach assesses climatic niche conservatism in reduced environmental space (PCA-env; Broennimann et al., 2012), while accounting for differences in the availability of climatic conditions and sampling effort (Broennimann et al., 2012; Guisan et al., 2014).

For each species separately, we calibrated a principal component analysis (PCA) on the 19 bioclimatic variables of the native and the invaded range. We used the scores of the first two PCA axes to create a two-dimensional climatic space, which we divided into a 100×100 grid (Guisan et al., 2014). We calculated smoothed occupancy of climatic conditions using the PCA scores for the climates and occurrences in both ranges ('ecospat' package; Di Cola et al., 2017).

We used the resulting smoothed occupancies of climatic conditions across the native and invaded ranges, to calculate representative metrics of climatic niche conservatism; because climatic niches have multiple ways of being dissimilar (Guisan et al., 2014; Liu et al., 2020). We used metrics of climatic niche conservatism that accounted for climatic conditions present in both the native and invaded range (analogue conditions), and for climatic conditions exclusive to one of them (non-analogue conditions), for two reasons. First, occupancy of non-analogue conditions could affect the accuracy of predictive models (Carlin et al., 2023). Second, given the diversity of climates on Earth, the occupancy of non-analogue climatic conditions may be an important niche component (Atwater et al., 2018; Carlin et al., 2023).

We calculated five components of climatic niche conservatism between the native and the invaded range: niche overlap, unfilling, stability, expansion and pioneering (Figure 1). Niche overlap was calculated as Schoener's *D*, which is the overlap in niche occupancy between the native and the invaded range, expressed as a proportion (0 = no overlap, 1 = complete overlap). To calculate niche overlap, we did not correct occurrence densities by the density of available climate in either range, since previous authors have linked such a correction to artefacts (Datta et al., 2019). The remaining components

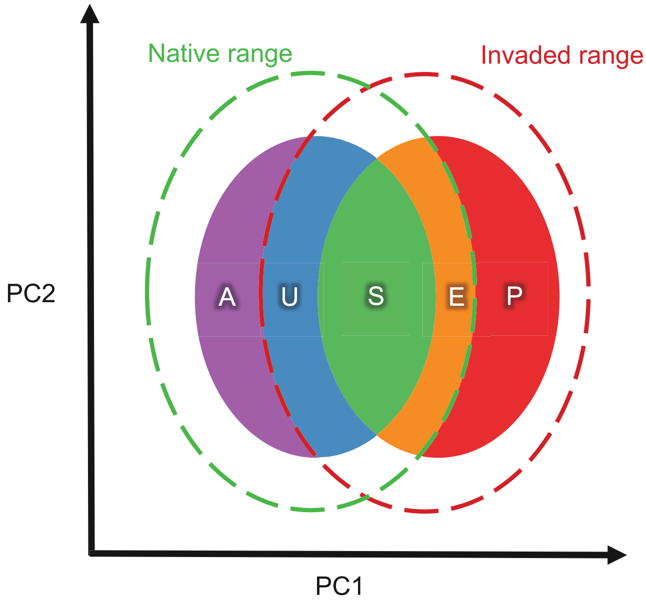

FIGURE 1 Diagram of the climatic niche conservatism components between the native and the invaded ranges of non-native plants in two principal components (PC) ordination axes. Available climatic conditions are shown with dashed lines (green for the native range, red for the invaded range). Occupied climatic conditions are shown with solid colours, with labels: A = abandonment, U = unfilling, S = stability, E = expansion, P = pioneering. Abandonment and Pioneering involve non-analogue climatic conditions (available only in either the native or the invaded range), while unfilling, stability and expansion involve analogue climatic conditions (present in both the native and invaded ranges). The abandonment component was omitted in the model presented in the main text, we further note that modelling abandonment did not influence conclusions (Figure S1). This diagram was based on previous works (Atwater et al., 2018; Guisan et al., 2014).

divided the whole niche occupancy (native and invaded range; Figure 1) into: unfilling (occupancy of climatic conditions available in both ranges, but only occupied in the native one), stability (occupancy of climatic conditions available and occupied in both ranges), expansion (occupancy of climatic conditions available in both ranges, but only occupied in the invaded one) and, finally, pioneering (occupancy of climatic conditions available only in the invaded range). For illustrative purposes, we also calculated abandonment (occupancy of climatic conditions available only in the native range), which did not influence conclusions on the correlates of niche conservatism (Figure S1). We note that niche overlap, abandonment and pioneering were concerned with non-analogue climatic conditions, while the rest of metrics were concerned with analogue climatic conditions. We used the 'ecospat' package (Di Cola et al., 2017), and functions kindly provided by Dr. Blaise Petitpierre (https://github.com/ecospat/ecospat/issues/65).

To assess how removal of marginal climates affected conclusions, we used climatic conditions up to the 100th, the 90th and the 75th quantiles (Guisan et al., 2014; Hill et al., 2017). Among different quantiles, changes in coefficients' significance were very rare, and the relative importance of variables did not change (Figure S2). Therefore, we present results with the 75th quantile, since they would be the least influenced by marginal climates.

To assess the overall level of niche conservatism, we calculated the percentage of non-native plants in which stability accounted for more than half of niche occupancy (Liu et al., 2020). Furthermore, to facilitate comparisons with previous studies, we calculated the percentage of species that had values of unfilling, expansion or pioneering >10%. This percentage has been used as a partly arbitrary threshold indicating relevant low levels of niche conservatism; in other words, a significant 'niche shift' (Dellinger et al., 2016; Hill et al., 2017; Petitpierre et al., 2012). We did not consider niche overlap as an unequivocal indicator of a niche conservatism on its own because it could be influenced by niche abandonment (Figure S3).

2.4 | Explanatory variables of climatic niche conservatism

For each of the 158 plant species we gathered data on their introduction pathway, minimum residence time, growth form and climatic niche breadth in their native range. The final sample size was 163 because five plant species were introduced through two different pathways and were thus duplicated in the dataset.

The introduction pathway categories were gardening ($n = 89$) and unintentional ($n = 74$) and were taken from published databases (Aymerich & Sáez, 2019; Sanz-Elorza et al., 2004).

Minimum residence time was the difference between 2021 and the year of first record outside cultivation, from the First Record Database v2.0 (Seebens, 2021; Seebens et al., 2018). In case a species was not included in this database, it was consulted in other sources (Anthos., 2021; Campos & Herrera, 2009; Riera et al., 2021, 2024; Romero, 2007; Sanz-Elorza et al., 2008, 2011; Sanz-Elorza, González, & Serreta, 2009).

Growth form accounted for longevity and growth habit, and we used the categories: annual herb ($n = 47$), perennial herb ($n = 70$), shrub or tree ($n = 46$). We classified prostrated succulents as perennial herbs, and arborescent succulents as shrub or tree. We took growth form from Sanz-Elorza et al. (2004).

Native climatic niche breadth was obtained by calculating a PCA with the climatic values of the native occurrences (19 bioclimatic variables), and aggregating the standard deviation of the scores of the first five axes with the geometric mean (Palma et al., 2021).

Unintentionally introduced plants were disproportionately more likely to be annual herbs and less likely to be shrubs or trees, compared with gardening plants (Figure S4 and Table S4). Plants with the widest climatic niches in their native range were introduced unintentionally and were annual herbs, although these covariations were weaker.

2.5 | Statistical analyses

We modelled the effect of introduction pathways, minimum residence time, growth form and native climatic niche breadth on niche overlap by fitting a mixed-effects beta regression, with fixed precision and a logit link ('glmmTMB' package; Brooks et al., 2017). We chose the beta regression because it is suitable for continuous proportions that do not arise from counts (Douma & Weedon, 2019). We accounted for phylogenetic relatedness by fitting random intercepts (species nested within genus, nested within family, taken from: Sanz-Elorza et al., 2004). We note that the variance component of taxonomic family was very close to zero (singular fit), but we chose to keep it because the phylogenetic non-independence is part of our study design. We quantified explained variation through the marginal and conditional R^2, which are, respectively, the variation explained by the fixed effects, and by the fixed and random effects ('MuMIn' package; Bartoń, 2023).

We modelled the effect of introduction pathways, minimum residence time, growth form and native climatic niche breadth on the other four climatic niche conservatism components (unfilling, stability, expansion and pioneering) by fitting a Dirichlet regression, which is a suitable method to model continuous proportions which are split among more than two categories (Douma & Weedon, 2019). We implemented the 'alternative' parametrization, which modelled (i) the four expected proportions under the constraint that they must sum up to one (unfilling was the base category with coefficients = 0; multinomial logit link), and (ii) precision (density around expected proportions; log link; Figure S2 and Table S5). We transformed the raw proportions to prevent exact zeroes and ensure the four proportions summed up to one ('DirichletReg' package; Maier, 2021). We accounted for phylogenetic relatedness by including phylogenetic covariates: ordination axes representing phylogenetic relationships (Supporting Information: Methods), obtained from a principal coordinate analysis on a matrix of phylogenetic distances (Desdevises et al., 2003; Jin & Qian, 2019). We quantified explained variation with a pseudo-R^2: we calculated the squared Spearman's correlation between the fitted values and the transformed proportions, and calculated the mean across the four components.

Our modelling strategy followed four steps. We first (1) built models without interactions: mixed-effects beta regression for niche overlap and Dirichlet regression for the remaining climatic niche conservatism components. We scaled continuous explanatory variables to: mean = 0, standard deviation = 1. The inclusion of quadratic terms was not supported by the Akaike Information Criterion corrected for small sample sizes (AICc; Table S6). The resulting models fitted the data (likelihood-ratio test: $p < 0.01$). Collinearity was low in the mixed-effects beta regression (variance inflation factors <2), while collinearity could not be assessed in the Dirichlet regression.

After building models without interactions, (2) we assessed whether the AICc supported the addition of a pairwise interaction, in two separate models: minimum residence time × introduction pathway, minimum residence time × growth form. We then (3) interpreted the supported models by plotting predictions and used estimated marginal means for the model of niche overlap ('emmeans' package; Lenth, 2023). Finally, we (4) approximated the relative importance of variables with dominance analysis, which calculates the proportional contribution of each explanatory variable to the model's total explained variation ('domir' package; Luchman, 2023).

To improve the interpretation of niche pioneering, which by definition partly depends on the availability of climates on the Earth's surface, we fitted two additional models with the same modelling strategy. First, we tested the correlates of the incidence of niche pioneering (niche pioneering greater than zero: yes/no) by fitting a binomial generalized linear mixed model to the subset of plants that have an invaded niche that is not completely nested within the native one ($N = 78$). Second, we assessed whether the same correlates could explain the extent of niche pioneering among the plants with niche pioneering greater than zero by fitting a mixed-effects beta regression ($N = 48$).

All data handling and statistical analyses were done in R (R Core Team, 2022).

3 | RESULTS

3.1 | Overview of climatic niche conservatism components

Climatic niche conservatism between the native range and the invaded range in Spain was substantial: stability accounted for more than half of niche occupancy in 87% of species (mean = 0.754; Figures 2 and S5). Unfilling was generally low (mean = 0.153, 54% of species <0.1), and twice as large as expansion and pioneering (mean = 0.062 and 0.031, respectively, more than 80% of species <0.1). Overall, 61% of species showed some evidence of substantially low niche conservatism (unfilling, expansion or pioneering >0.1). Niche overlap was mostly low (mean Schoener's $D = 0.246$; Figure 3 and Figure S3).

3.2 | Correlates of climatic niche conservatism components

Native climatic niche breadth was the most important variable influencing climatic niche conservatism, because it accounted for 57% of the explained variation of niche overlap (mixed-effects beta regression, $R^2_{marginal} = 0.179$), and for 50% of the explained variation of the other climatic niche conservatism components (Dirichlet regression, pseudo-$R^2 = 0.219$). Niche overlap decreased by more than half between the species with the narrowest and the widest climatic niche in their native range (model's predictions; Figure 3). Climatic niche conservatism components changed with increasing native climatic niche breadth: stability increased 18%, expansion and pioneering decreased by 9% and 8% (respectively), unfilling changed around 1% (model's predictions, Figure 4).

Growth form was more important for niche overlap than for the other climatic niche conservatism components: 34% versus 14% of explained variation. Shrubs and trees tended to have 7% less niche overlap than perennial herbs (Tukey contrast on estimated marginal

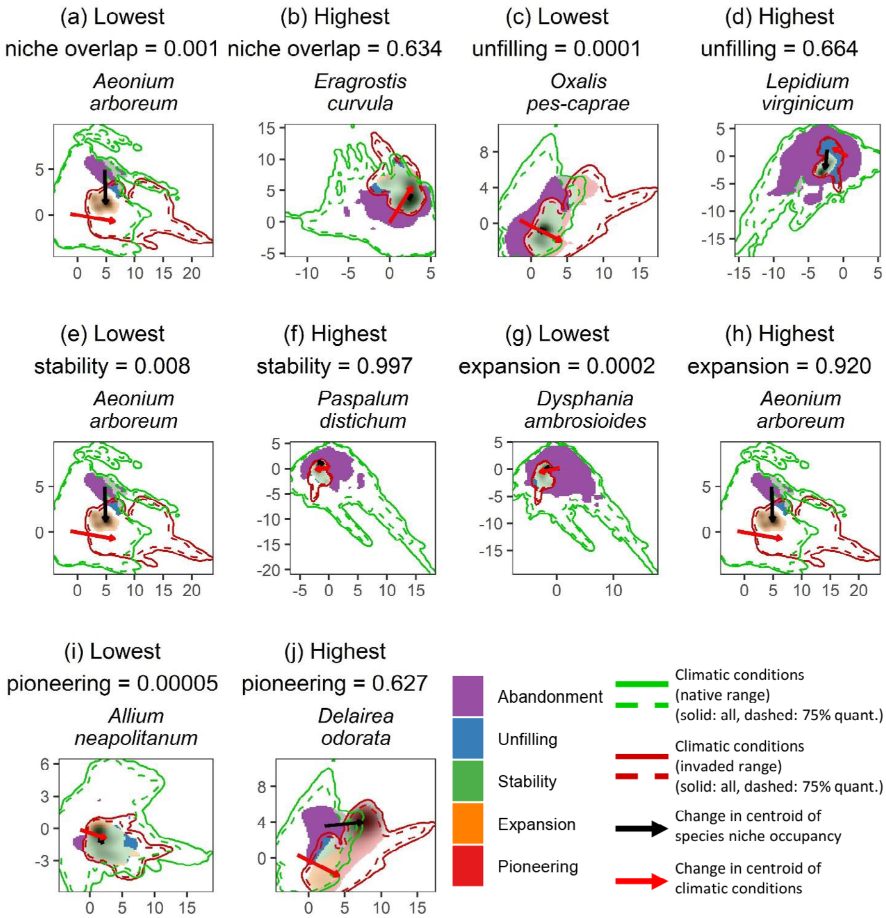

FIGURE 2 Climatic niches of plant species between the native and invaded ranges, in reduced ordination space (principal component analysis axes), showing only extreme values of metrics of niche conservatism (a-j). We note that this figure shows the lowest non-zero value, since some taxa had zero unfilling, expansion or pioneering. Darker shading indicates greater niche occupancy in the invaded range, while grey colour indicates climatic conditions removed from the calculation of niche conservatism metrics, because of their marginality. See Figure S5 for the climatic niches of all species. quant. = quantile.

means: *p*-v = 0.024), and marginally less overlap than annual herbs (9% difference, *p*-v = 0.049; Figure 3). Moreover, shrubs and trees tended to have 10% less stability than annual and perennial herbs and 7% more unfilling (model's predictions; Figure 4), but similar expansion and pioneering (around 1%–2% change). Neither niche overlap nor the other climatic niche conservatism components were explained by the interaction between growth form and minimum residence time (both: ΔAICc >2, Table S8).

Niche overlap was not related to minimum residence time (95% confidence interval included zero, 9% of explained variation, Figure 3; Table S7). However, minimum residence time influenced the other climatic niche conservatism components (26% of explained variation). Compared with the newest introductions, the oldest introduced species tended to have 15% more stability and 14% less unfilling, while change in expansion and pioneering was around 1% (model's predictions; Figure 4).

Introduction pathway was not important for niche overlap nor the other climatic niche conservatism components (respectively: 0% and 3% of explained variation; both: 95% confidence intervals included zero; Figures 3 and 4). The interaction between introduction pathways and minimum residence time did not explain niche overlap nor the other climatic niche conservatism components (both: ΔAICc >2, Table S8).

Phylogenetic relatedness was important for niche overlap, because the random effect of taxonomy (species nested within genus, nested within family) increased the explained variation four-fold ($R^2_{marginal}$ = 0.179; $R^2_{conditional}$ = 0.689). In comparison, phylogenetic relatedness contributed little to the explained variation on the other niche conservatism components (phylogenetic axis 8: 7%), but still was twice as much as introduction pathways.

Among those plants whose invaded climatic niche was not completely nested within the native one (around half of the full dataset), the incidence of niche pioneering was negatively related to the breadth of the native climatic niche (binomial GLMM, $R^2_{marginal}$ = 0.303; $R^2_{conditional}$ = 0.355, Table S9). The other variables in our models (including some pairwise interactions) did not explain the incidence of niche pioneering, nor the extent of niche pioneering among those plants with non-zero pioneering (mixed-effects beta regression, Table S9).

4 | DISCUSSION

Climatic niche differences between the native range and the invaded range in mainland Spain were characterized by high levels of niche stability together with frequent shifts but mostly of small magnitude, while niche overlap was mostly low. Introduction pathways were not correlated to any of the climatic niche conservatism components. Climatic niche conservatism was highest for annual and perennial herbs, plants introduced a long time ago, and those

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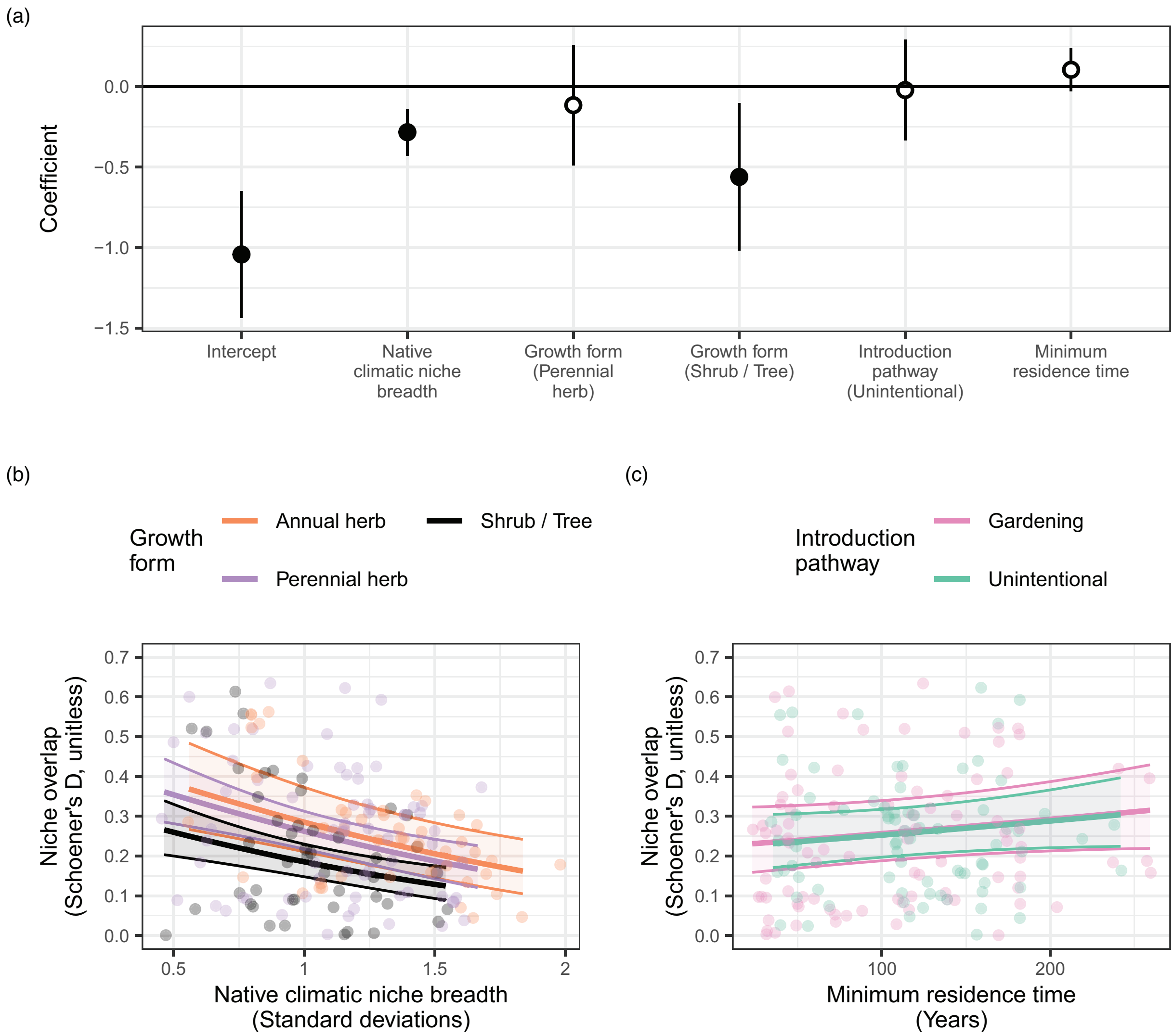
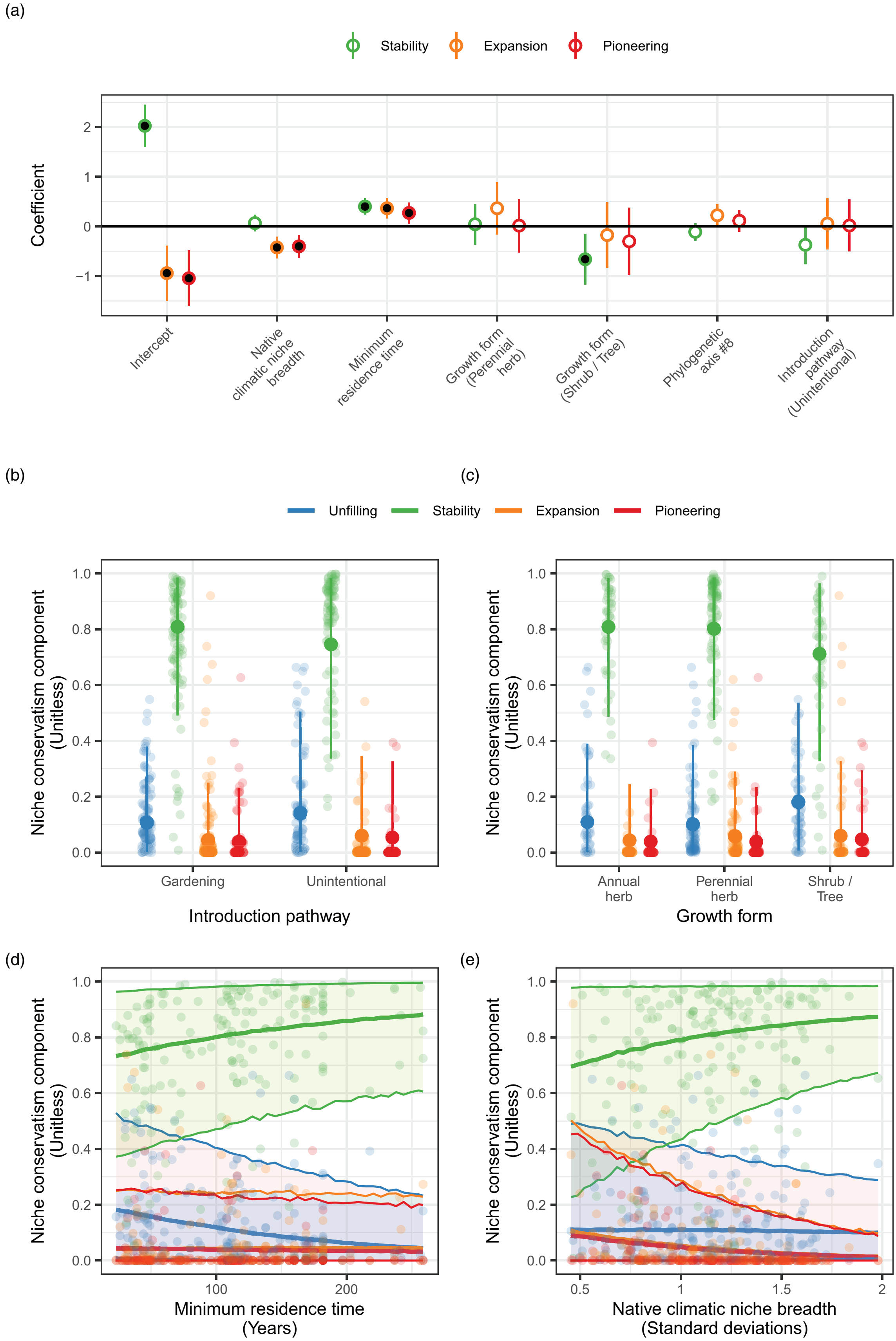


FIGURE 3 Correlates of niche overlap (Schoener's *D*), as modelled by a mixed-effects beta regression (species nested within genus, nested within family), using data up to the 75th quantile. (a) Coefficients at the logit scale, those that included zero in their 95% confidence intervals have white filling. The intercept is the mean niche overlap of plants with the mean value of numerical covariates, and the reference categories of annual growth form, and gardening introduction pathway. (b and c) Predicted relationships between niche overlap and explanatory variables (with 95% confidence bands, avoiding extrapolation). Dots depict non-native plant species, with added noise and transparency for visualization. *N* = 163 (158 plants. Five duplicated since they were introduced through two pathways). See Table S7 for the coefficients.

with wide climatic niches in their native range. Climatic niche conservatism was not driven by relevant interactions of introduction pathways nor growth form with minimum residence time. The most important factor influencing climatic niche conservatism was native climatic niche breadth, suggesting that conservatism was more influenced by a species' ability to cope with broad climatic conditions rather than processes related to introduction history or growth form.

4.1 | Overview of climatic niche conservatism

Stability was the dominant niche conservatism component, largely supporting the niche conservatism hypothesis, which posits that species tend to retain their niche in time and space (Liu et al., 2020; Petitpierre et al., 2012). Furthermore, our finding of conserved climatic niches are consistent with the invasion of similar habitats between ranges (Kalusová et al., 2013). Niche overlap between the native and the invaded ranges was mostly low, congruent with previous work on non-native plants (Dellinger et al., 2016; Sychrová et al., 2022); largely due to abandonment of climatic conditions exclusive to the native range. The incidence of niche shifts (61% of species) suggested that high levels of conserved niches can co-occur with niche shift, although such niche shifts were of small magnitude on average. Around 40% of plants had relevant levels of niche unfilling, indicating a potential to occupy more climatic space in the invaded range (Gassó et al., 2012; Liu et al., 2020). Moreover, plants rarely expanded their niche into climatic conditions that were



available but not occupied in their native range, and the pioneering into climatic conditions that were not available in their native range was even rarer. This was possibly due to fitness trade-offs among traits, lack of sufficient genetic diversity or dispersal limitations, which prevented occupancy of more extreme climatic conditions (Alexander & Edwards, 2010).

FIGURE 4 Correlates of the other niche conservatism components, as modelled by a Dirichlet regression, using data up to the 75th quantile. (a) Coefficients at the multinomial logit scale, those that included zero in their 95% confidence intervals have white filling. The intercept is the mean niche conservatism component of plants with the mean value of numerical covariates, and the reference categories of annual growth form, and gardening introduction pathway. (b–e) Predicted niche conservatism components, which always sum up to one for each factor level (b and c) and each value of the numerical covariates (d and e). Confidence bands around predicted trends (thick line) are 95% prediction intervals obtained through simulation (Douma & Weedon, 2019). To aid visualization, dots depict non-native plant species with added transparency and random noise (four dots per species), and in panels (b and c), niche conservatism components are plotted side-by-side for each factor level. $N = 163$ (158 plants. Five duplicated since they were introduced through two pathways). See Table S5 for the coefficients.

4.2 | Climatic niche conservatism is not strongly related to introduction pathways

Contrary to our expectation, and partly in contrast with previous studies (Atwater et al., 2018; Liu et al., 2020), all of the studied niche conservatism components were not strongly related to introduction pathways. An analysis considering non-analogue climates at the global scale found that wide cultivation correlated to reduced niche overlap, stability and unfilling, and increased expansion (compared with plants that were not cultivated; Atwater et al., 2018). In contrast, in a meta-analysis considering only analogue climates, a combination of intentional and unintentional introduction led to greater niche similarity and stability, but similar expansion and unfilling (compared with plants introduced only intentionally or only unintentionally; Liu et al., 2020). Our work therefore suggests that the effect of introduction pathways on niche conservatism could be context-dependent.

Moreover, we did not find relevant interactions between pathways and residence time affecting niche conservatism. The similar niche conservatism among plants introduced through different pathways could relate to multiple explanations. First, introduction pathways are proxies of initial conditions of introduction that can become less relevant to explain invasion patterns as residence time increases (Donaldson et al., 2014; Kempel et al., 2013). Second, we possibly lacked statistical power to detect small effects. Third, introduction pathways were stronger proxies of growth form than native climatic niche breadth (Riera et al., 2024), while the latter was more strongly related to niche conservatism than growth form.

4.3 | Other correlates of climatic niche conservatism

Growth form was a relevant correlate of climatic niche conservatism, with effects contrary to our expectations: Annual and perennial herbs showed more niche stability and overlap than shrubs and trees. Our result agrees with previous findings (Atwater et al., 2018), while other studies found no relationship between niche conservatism and longevity or growth form (Gallagher et al., 2010). The greater niche conservatism among herbs could arise due to wider niches in the native range compared with shrubs and trees (Riera et al., 2024), since a wide niche correlated to more stability (see below). Moreover, the lower niche conservatism for shrubs and trees could relate to covariation with introduction pathways: shrubs and trees were disproportionately likely to be cultivated (Atwater et al., 2018; Riera et al., 2024), which previous work has linked to less stability and overlap (Atwater et al., 2018). Therefore, while we could not recover an individual or interacting effect of pathways on niche conservatism, we cannot rule out an indirect effect through a covariation with growth form (Atwater et al., 2018).

In any case, our results do not support reduced niche conservatism among herbs due to more 'evolutionary potential' (i.e. faster rates of molecular and niche evolution; Lanfear et al., 2013; Smith & Beaulieu, 2009). The interaction between growth form and minimum residence time was not an important correlate of niche conservatism, contrary to our expectations, but similarly to previous work (Early & Sax, 2014). The lack of correlation could be due to differences of scale: Faster rates of molecular and climatic niche evolution above the genus level across millions of years (Lanfear et al., 2013; Smith & Beaulieu, 2009) do not necessarily translate into reduced niche conservatism at the species level across two and a half centuries of invasion. Moreover, other works approximating 'evolutionary potential' found similar niche conservatism between apomictic and sexually reproducing plants (Dellinger et al., 2016). A more proximal test of the role of 'evolutionary potential' on niche conservatism would require data on genetic diversity, and the incidence and magnitude of post-introduction evolution (Dellinger et al., 2016).

The importance of minimum residence time on climatic niche conservatism indicates the need of considering the dynamic nature of invasions. As we expected, there was more niche conservatism among older introductions, partly in contrast to previous works (Early & Sax, 2014; Gallagher et al., 2010; Liu et al., 2020; Petitpierre et al., 2012; Sychrová et al., 2022). Niche overlap was unrelated to minimum residence time, similarly to previous works on analogue climates (Liu et al., 2020; Petitpierre et al., 2012; Sychrová et al., 2022). Our results provide new insights on patterns of geographical spread and niche breadth. Plants with more residence time tend to achieve greater range size and niche breadth in the invaded range (Banerjee et al., 2021; Gassó et al., 2009; Riera et al., 2024). Since we observed increasing stability and decreasing unfilling with increasing residence time, our results suggest that spread in geographic and climatic space in the invaded range mostly takes place by invading climatic conditions similar to the ones in the native range.

The overwhelming correlate of niche conservatism was the breadth of the climatic niche in the native range: plants with wider native climatic niches had more niche conservatism, as we expected (Dellinger et al., 2016; Early & Sax, 2014; Sychrová et al., 2022; but see Gallagher et al., 2010). Indeed, plants with wide niches were less likely to experience niche pioneering. Plants with a narrow niche in the native range had more climatic space left to occupy, and their capacity to achieve greater expansion and pioneering could relate to pre-adaptation (Carlin et al., 2023; Petitpierre et al., 2012), post-introduction evolution of adaptation (Early & Sax, 2014) or to an enhancement of their dispersal by human activity (Carlin et al., 2023). The major importance of native climatic niche breadth suggests that plant physiological tolerances arising through natural selection in the native range were more important than features of the introduction process in the invaded range.

Additional factors outside our scope could influence our results. We showed that accounting for phylogenetic relatedness increased explained variation in niche conservatism, a pattern that has not been analysed before (Atwater et al., 2018; Dellinger et al., 2016). Therefore, niche conservatism could be influenced by phylogenetically correlated variables which we did not include in our models (Ives, 2022), such as functional traits (Vásquez-Valderrama et al., 2022). Niche conservatism can also be influenced by biotic interactions; for instance, the release from herbivores and fungi could allow colonizing environmental conditions that were unoccupied in the native range (DeWalt et al., 2004). Furthermore, the inclusion of non-climatic variables, such as anthropogenic disturbance, could yield further insights (González-Moreno et al., 2015). The role of such variables could be particularly important to explain the extent of niche pioneering among those with non-zero pioneering, since this extent could not be explained by any of the correlates tested in this study.

4.3.1 | Caveats and limitations

The analysis of niche conservatism faces multiple challenges. On the one hand, some bias is inherent to large biodiversity databases, such as GBIF (Meyer et al., 2016), and while we sought to minimize such bias by filtering the GBIF download (Zizka et al., 2019), it is possible that some remains in our metrics of niche conservatism. Our choice of study area, and our use of political boundaries to outline native and invaded ranges, could also influence our results, as previous work shows that the metrics of niche conservatism are influenced by how the native and invaded ranges are outlined (Hill et al., 2017; Mateo et al., 2015). Furthermore, the interpretation of niche pioneering is somewhat challenging, as it partly depends on the availability of climates (Guisan et al., 2014). We therefore opted to separately model the incidence and extent of such niche shifts, keeping only the relevant subset of non-native plants with an invaded niche that is not completely nested within the native one.

5 | CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

Our work illuminates how niche conservatism is associated with introduction-related factors and species' biological attributes. The most important correlate of niche conservatism was native climatic niche breadth, rather than introduction pathways, growth form or minimum residence time. Furthermore, we identified which variables influenced changes in stability and unfilling, which are two niche conservatism components with positive and negative effects on the ability of ENMs to predict non-native plant' spread (Liu et al., 2022). Ecological Niche Models would be most reliable for herbs, species introduced a long time ago, and with wide climatic niches in their native range. Further research is needed into the correlates of niche conservatism among non-native plants, given the accelerating pace of new invasions (Seebens et al., 2018), and ever increasing negative impacts (Bacher et al., 2024).

AUTHOR CONTRIBUTIONS

Marc Riera led data gathering, data analysis and manuscript writing. All authors contributed equally to manuscript conception. All co-authors reviewed the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All occurrences were gathered from the Global Biodiversity Information Facility (GBIF, 2021). The datasets and code that reproduce our results are available on the CORA repository: https://doi.org/10.34810/data1716 (Riera et al., 2025).

STATEMENT ON INCLUSION

Our study relied on species occurrences data at the global extent, downloaded from the public database GBIF. Therefore, there was no local data collection. Our GBIF download was created through a DOI, and thus rewards scientists and data-publishing institutions world-wide by recognizing the value of open biodiversity data and demonstrating its impact on their funders and stakeholders.

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SUPPORTING INFORMATION

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

Figure S1. Correlates of niche conservatism components, including abandonment, as modelled by a Dirichlet regression, using data up to the 75th quantile.

Figure S2. Coefficient across removal of marginal climates (3 shapes), and modelling of interactions (3 colours of vertical bars, which represent 95% confidence intervals), for models of: (a) niche overlap (logit scale, mixed-effects beta regression), (b) other niche conservatism components (Dirichlet regression, expected proportions have coefficients at the multinomial logit scale, while precision was at the log scale).

Figure S3. Correlation among the niche conservatism components, including abandonment: scatterplots (lower triangle, with added transparency for visualization), and Spearman's correlation (upper triangle).

Figure S4. Covariation between explanatory variables (only those significant among all pairwise tests; see Table S4).

Figure S5. Climatic niches of plant species between the native and invaded ranges, in reduced ordination space (Principal Component Analysis axes).

Table S1. Overview of previous studies on drivers of niche conservatism of non-native plants (ordered from oldest to newest); focusing on the aspects that we think are most relevant to compare to our study.

Table S2. Plants with edited native ranges: the removed regions were not part of the native background climate, nor did they contribute occurrences.

Table S3. Level 2 polygons removed from the definition of background climate: while they were part of the native range according to the Plants of the World Online webpage (POWO, 2021), they lacked GBiF occurrences.

Table S4. Pairwise covariation between explanatory variables, assessed through a calculation of effect size and a significance test.

Table S5. Coefficients of variables driving the other niche conservatism components (Dirichlet regression; Figure 4 in the main text).

Table S6. Effect of quadratic terms on the Akaike Information Crtierion corrected for small sample sizes (AICc), across three levels of removal of marginal climates, in: (a) models of niche overlap (mixed-effects beta regression), (b) models of the other niche conservatism components (Dirichlet regression).

Table S7. Coefficients of correlates of niche overlap (mixed-effects beta regression, genus nested within family; Figure 3 in the main text).

Table S8. Effect of adding interactions to models containing only additive effects, on the Akaike information criterion corrected for small sample sizes (AICc) and a metric of model quality ($R^2_{marginal}$ or pseudo-R^2, as appropriate). (a) models of niche overlap (mixed-effects beta regression), (b) models of the other niche conservatism components (Dirichlet regression).

Table S9. Coefficients of correlates of (a) the incidence of niche pioneering (binomial GLMM, $R^2_{marginal}=0.303$; $R^2_{conditional}=0.355$), and (b) the extent of niche pioneering (mixed-effect beta regression, $R^2_{marginal}=0.114$; $R^2_{conditional}=0.114$).

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