

# Invasive woody legumes: Climatic range shifts and their relationships to functional traits

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## Abstract

**Aim:** Analysis of the shifts in the climatic space for invasive species between native and introduced areas is a powerful tool for understanding their distribution patterns and the factors influencing their spread into new areas. In this study, we explored the shift in climatic distribution between ranges for invasive woody legumes and how the functional traits of these species are associated with their climatic distribution.

**Location:** Global.

**Time period:** Present.

**Major taxa studied:** Invasive woody legumes.

**Methods:** We evaluated the global patterns of occupation of the climatic space for 107 invasive woody legumes in their native and introduced distribution ranges, in addition to the differences in six key functional traits. We used the trait probability density (TPD) function to estimate species probabilistic niches. We then classified species into four groups according to the climatic differences between the distribution ranges. The comparisons between the climate shift groups and the distribution ranges were evaluated with mixed linear models. Additionally, we compared the functional traits between species groups using ANOVA.

**Results:** Overall, we found that invasive species exhibited low to moderate climatic overlap between their native and introduced distribution ranges. However, climatic conditions in the introduced range were different from those in the native range. Invasive legumes were clustered in four groups (conserved, expansion, dissociation and unfilling), with dissociation between climate niches being the most common one. In terms of functional traits, the most relevant finding was that the species in the expansion group had larger leaves than species in the dissociation group.

**Main conclusions:** Our results showed no consistent climatic range shift across all invasive woody legume species from their native to their introduced distribution. However, some species tended to invade climatic conditions that were different from those in their native range, supporting the hypothesis that some invasive species are able to adapt to novel environmental conditions. Finally, functional traits might be a good predictor of how these species modify their climatic spaces.

## KEYWORDS

climatic niche, climatic shift groups, functional traits, introduced range, invasive legumes, invasive plants, native distribution

## 1 | INTRODUCTION

Invasive plants have been introduced by humans in different parts of the world and represent an important threat for biodiversity conservation (Rejmánek & Richardson, 2013; Richardson & Rejmánek, 2011). In particular, there is great concern about the invasion of woody plants, of which 622 species (357 tree species and 265 shrubs) have been identified as invasive across the world (Richardson & Rejmánek, 2011). It has long been known that invasion is determined by the interaction between the environmental conditions of the areas of introduction and the characteristics of the species that determine their response to those environmental conditions, facilitating their establishment and invasion (Rejmánek, 1999). Studies on the distribution of invasive tree and shrub species have found that most of them are limited by factors such as climate, soil and nutrient availability, which affect their ability to survive in the new areas of introduction (Beauregard & De Blois, 2014; Peterson, 2003). Therefore, invasive plants can invade areas with adequate conditions for their permanence, generally in environments similar to those found in their native ranges (Kraft et al., 2015; Rejmánek et al., 2005). It is common for species distribution studies to focus on climatic variables, given that they are strong predictors of their distribution and they allow for rapid analysis and understanding of the relationship between the environment and distribution (Heikkinen et al., 2006; Thuiller et al., 2006). For these reasons, analysis of climatic space shifts for invasive species between native and introduced areas enables an understanding of the patterns of species distributions and the factors influencing new occupation areas (González-Moreno et al., 2014).

A large number of studies have estimated the overlap in environmental conditions between native and non-native ranges (introduced range), using direct observations and species distribution models (Broennimann et al., 2012; Guisan et al., 2014; Petitpierre et al., 2012). However, owing to the low number of species included in most of these studies, generalizations are difficult (Fernández & Hamilton, 2015; Guisan et al., 2014), and the described patterns have shown contradictory behaviour of the invasive species. Some studies have described high overlap in environmental conditions between native and introduced distributions (Petitpierre et al., 2012; Sexton et al., 2009), whereas others have found low overlap, concluding either that native and introduced distributions occupy separate parts of the environmental space or that the introduced range represents an expansion of the native one (Beaumont et al., 2009; Perret et al., 2018; Turner et al., 2015). Additionally, most studies have considered only one part of species distribution (climate), omitting the fact that species characteristics (functional traits) related to invasion can modulate the distribution and response of the plants across environmental conditions (Carboni et al., 2017; Fernández & Hamilton, 2015).

It is unclear whether certain traits of invasive plants might be associated with the conservation of the climatic space between native and introduced distribution ranges. Growth forms of invasive plants can be related to changes in climate distribution between native and invaded areas, with shrubs and trees showing lower climate niche similarity than forbs (Atwater et al., 2018). However, Gallagher et al. (2010) did not find any association between the functional

traits of species and the shift in climate space between native and invaded ranges. Additionally, some studies have described that invasive species present novel functional strategies that make them succeed in different environments and can even shift the mean values of their functional traits along different environmental conditions (Treurnicht et al., 2020). For example, some invasive species might exhibit functional traits associated with rapid acquisition of resources (i.e., high specific leaf area and large plant height) in high-resource environments, but “conservative” traits in environments with limited resources (Funk & Vitousek, 2007; Leishman et al., 2007). Also, it has been described that species adapted to stressful conditions, such as drought and extreme temperatures, in their native distribution area can hardly ever invade areas with more extreme environmental conditions in the introduced area (te Beest et al., 2013). Nevertheless, it is necessary to take into account that different functional traits can confer different advantages in different taxonomic groups or growth forms (Atwater et al., 2018).

Among the global list of invasive woody species identified by Richardson and Rejmánek (2011), the Fabaceae family is the one that encompasses the largest number of species (138) (Rejmánek & Richardson, 2013). This family has a wide distribution, being present on all continents and in all terrestrial biomes except Antarctica. Additionally, legumes are one of the most important plant families for humans, who use them for food production, fodder, medicines and timber (Bradshaw et al., 2008; Richardson & Rejmánek, 2011). Therefore, legumes represent a good opportunity to explore, in a large group of species, differences in climate between native and introduced ranges and whether these differences are associated with functional traits. Here, we ask two main questions. First, how do the native and introduced climatic distributions differ for invasive woody legumes? We expect that the native and introduced distributions of invasive woody legumes will show high similarity in their climatic conditions (i.e., niche conservatism). Second, how are functional traits of invasive woody legumes associated with their climatic distribution? We expect that invasive woody legumes whose native distribution is associated with extreme climatic ranges (e.g., cold environments, high temperatures and drought areas), will show a high climatic niche conservatism and conservative functional traits (e.g., high wood density, high leaf dry matter content and lower height). In contrast, invasive plants coming from non-extreme climates will exhibit a shift in climate distribution between the native and introduced ranges and possess acquisitive functional traits (e.g., low wood density and leaf dry matter content, and large leaf area and height).

## 2 | METHODS

### 2.1 | Occurrence data

Considering that Fabaceae is the most prominent invasive family across the world, for this study we selected the 138 invasive woody legume species listed as invasive by Rejmánek and

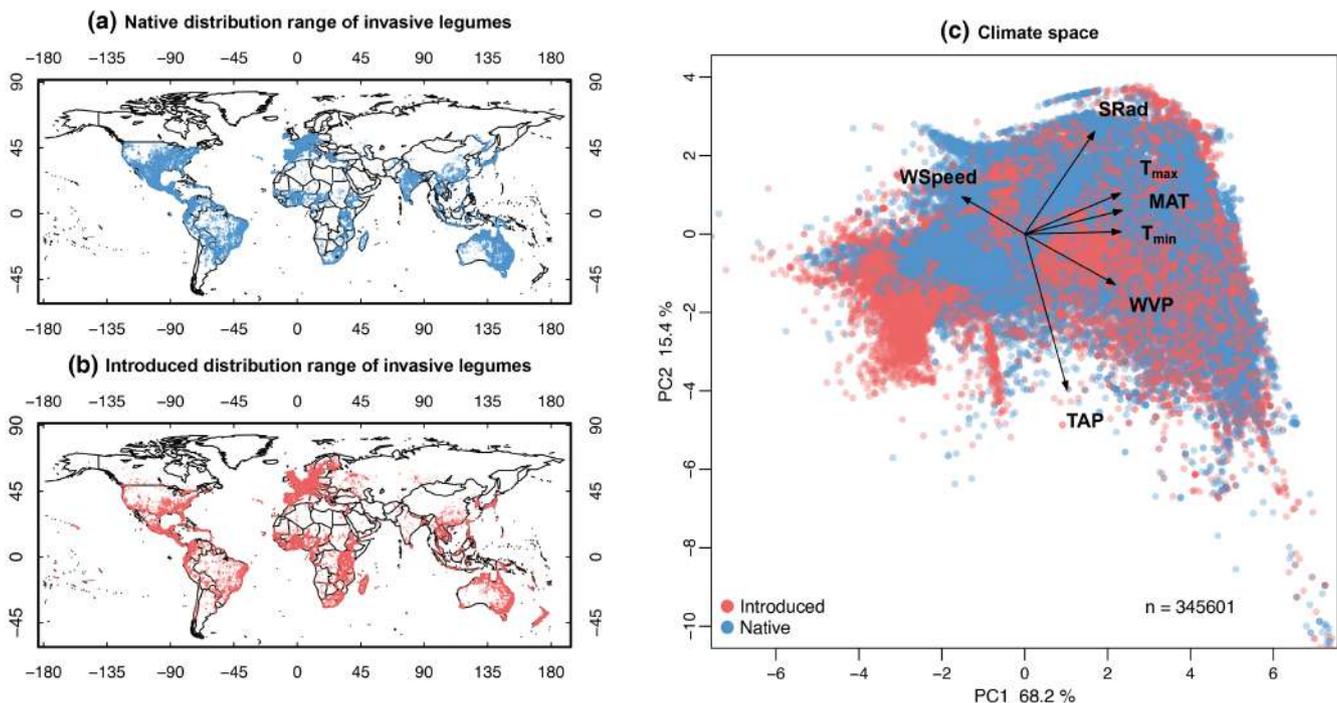
Richardson (2013). The species names and synonyms were standardized using the The Plant List database (<http://www.theplantlist.org>; see Appendix). We collected occurrence data for all accepted names and synonyms from the Global Biodiversity Information Facility (GBIF), using the R package *rgbif* (Chamberlain et al., 2019). We obtained a total of 790,858 occurrences, which we thoroughly revised and verified, eliminating occurrences without geographical coordinates, duplicated coordinates, locations outside continents and islands and outliers according to Maldonado et al. (2015), using R companion to Geographic Information Analysis (<https://rsatial.org/rosu/index.html>). Additionally, we searched the native distribution of species in the Invasive Species Compendium (CABI) database and the International Legume Database & Information Service (ILDIS) and included the continent and countries. It is important to mention that the native origin of species in this study is established while considering the resolution of the country. This means that we were not able to detect cases in which the species are native and invasive in the same country (Richardson & Rejmánek, 2011). All occurrences were classified as being in the native or introduced range (Figure 1a,b). The Supporting Information (Table S1) includes the complete list of species and their origins. Finally, we removed 31 species without occurrences or with fewer than five occurrences, resulting in a database of 345,601 occurrences distributed in 107 species.

## 2.2 | Climate data

We downloaded climate data for species occurrences from WorldClim v.2.0 (30', c. 1 km<sup>2</sup> spatial resolution; Fick & Hijmans, 2017; see Appendix). We selected only climatic variables used for the spatial interpolated model and observed directly from weather stations (Supporting Information Table S3). The variables included mean annual solar radiation (SRad, in kilojoules per square metre), total annual precipitation (TAP, in millimetres), maximum mean annual temperature ( $T_{\max}$ , in degrees Celsius), mean annual temperature (MAT, in degrees Celsius), minimum mean annual temperature ( $T_{\min}$ , in degrees Celsius), mean annual water vapour pressure (WVP, in kilopascals) and mean annual wind speed (WSpeed, in metres per second).

## 2.3 | Functional traits

We compiled information on six functional traits commonly associated with growth, survival and reproduction of plants (Díaz et al., 2016). First, leaf area (LA, in square millimetres) is related to leaf energy and water balance (Díaz et al., 2016). In general, small leaves are typical in dry areas with high temperatures and at high elevations. In contrast, large leaves are common in wet and sunny environments



**FIGURE 1** Climate distribution of invasive woody legumes. The maps include 345,601 occurrences for 107 species based on the Global Biodiversity Information Facility (GBIF) data. All occurrences were classified as being in the native range or the introduced range. (a) Occurrences in the native distribution range of invasive legumes. (b) Occurrences in the introduced distribution range of invasive legumes. (c) The climate space of invasive woody legumes [first two components (PC1 and PC2) of the principal components analysis axes for climate variables], including all species and the native and introduced ranges. MAT = mean annual temperature; SRad = mean annual solar radiation; TAP = total annual precipitation;  $T_{\max}$  = maximum mean annual temperature;  $T_{\min}$  = minimum mean annual temperature; WSpeed = mean annual wind speed; WVP = mean annual water vapour pressure

(Peppe et al., 2011; Wright et al., 2017). Second, specific leaf area (SLA, in square millimetres per milligram) is related to photosynthesis and respiration, reflecting a trade-off between leaf construction costs and photosynthetic potential. High SLA values are reported in high-precipitation environments, and low SLA values are common when MAT is high (Díaz et al., 2016; Gong & Gao, 2019; Wright & Westoby, 2004). Third, leaf nitrogen (LN, in milligrams per gram) is positively correlated with photosynthetic and decomposition rates. Low LN is related to dry environmental conditions and high temperature (Reich, 2014; Wright & Westoby, 2004). Fourth, plant height ( $H$ , in metres), is correlated with plant life history, seed dispersal, plant life span and the ability to compete for light. In dry, very cold sites and at high elevations the PH is generally lower, and it tends to increase along with TAP (Díaz et al., 2016; Madani et al., 2018). Fifth, specific stem density (SSD, in grams per cubic centimetre) reflects the carbon investment by a plant in its stem, and it is related to xylem storage, mechanical support and water transport of plants (Chave et al., 2009). The SSD increases with increasing annual temperature and decreasing annual precipitation (Wiemann & Williamson, 2002). Sixth, seed mass (SM, in milligrams) is related to seedling competitiveness, dispersal, survival and colonization ability (Cornelissen et al., 2003; Díaz et al., 2016). The SM increases with increasing temperature and solar radiation (Murray et al., 2004). Functional trait values were obtained from the TRY database (<https://www.try-db.org/TryWeb/Home.php>, accessed April 2019; see the Appendix).

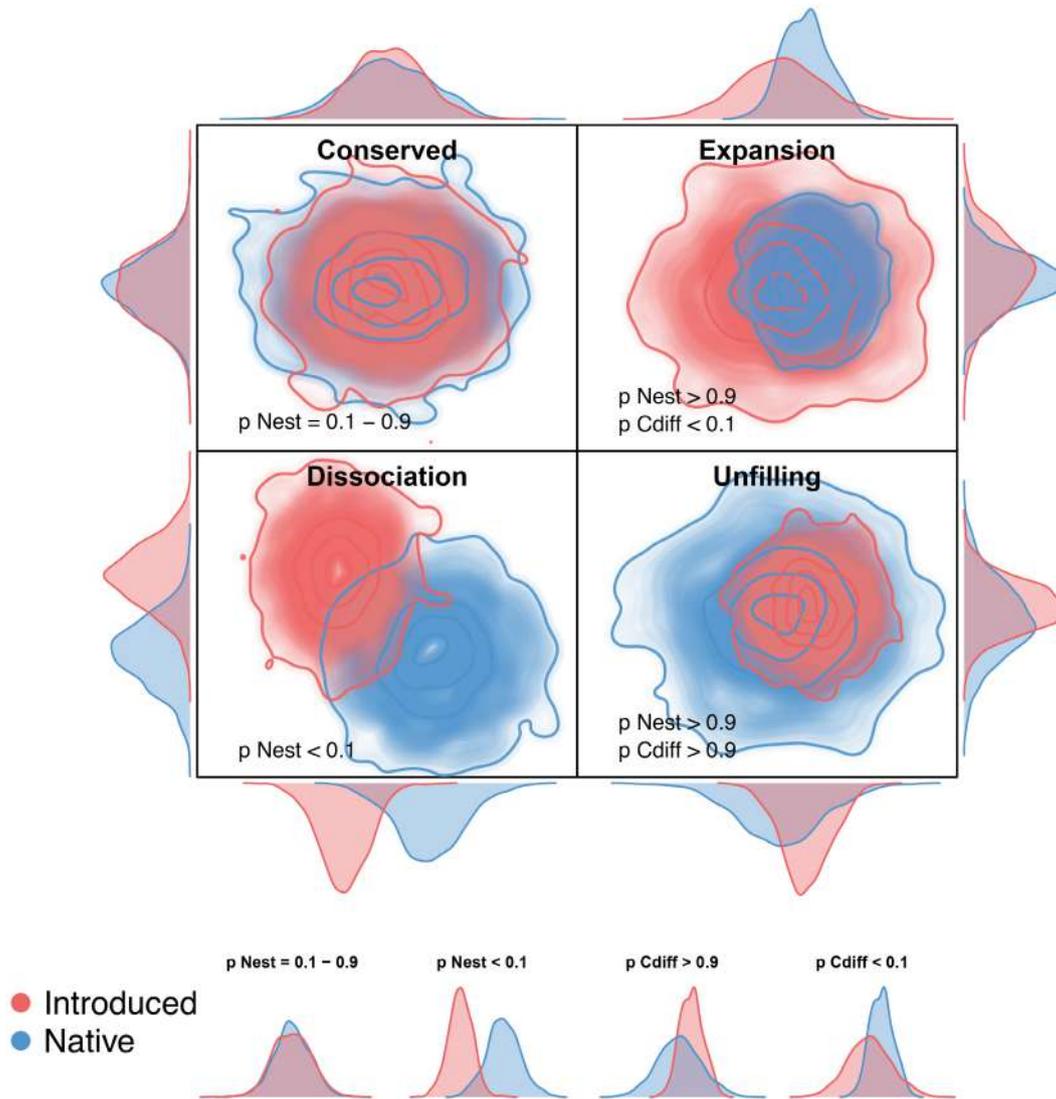
Following Carmona, Tamme, et al. (2021), for each species we estimated the average trait values of each trait, after excluding outliers (observations  $>3$  SD away from the species mean). The averages for each species–trait combination were calculated first within individuals (if multiple measurements were taken from a single individual), then within datasets (if multiple individuals were measured in the same location) and, finally, within species (if multiple individuals were measured at various locations). Given that some species did not have information for all traits, we performed a phylogenetically informed trait imputation using the R package *MISSFOREST* (Stekhoven & Bühlmann, 2012). Phylogenetic information was obtained using the R package *V.PHYLOMAKER* (Jin & Qian, 2019) and was included in the imputation by considering the first 10 phylogenetic eigenvectors in the matrix to be imputed, as recommended by Penone et al. (2014).

## 2.4 | Data analysis

To characterize the climatic spaces of species for both native and introduced ranges, we performed a principal components analysis (PCA) with the seven climate variables, scaled by z-normalizing with  $\mu = 0$ ,  $\sigma = 1$ . The first two components of the PCA explained 83.6% of the variance (Figure 1c). The first PCA axis (PC1; 68.2% of explained variance) was principally associated with temperature-related variables, whereas the second PCA axis (PC2; 15.4%) was associated with the TAP (Figure 1c). We used these two PCA axes (hereafter, “climate space”) to determine the climate niche of each species. We defined the native, introduced and total (i.e., considering both native

and introduced observations) climate niches of each species as the density of occupation of the climate space based on their occurrences in the climate space. Considering that the density of occupation is a more accurate way to assess niche areas than comparing only the boundaries of the niche occupied by species (Broennimann et al., 2012; Carmona et al., 2016; Carmona, Tamme, et al., 2021), we used a bivariate Gaussian probability kernel function to estimate this density; for each climate niche, we selected a bandwidth using the unconstrained bandwidth estimation described by Duong and Hazelton (2003). The value of the kernel function in each point of the climatic space reflects the density (in probabilistic terms) of the occurrences of a species in those climatic conditions. We applied a 99% probability threshold to reduce the effect of extreme outliers ( $\alpha = .01$ ; Carmona et al., 2019). Applying the threshold also allows the definition of areas of the climate space that are not occupied by probabilistic niches (by setting the density value to zero in points below the probability threshold), which, in turn, allows exploration of how much of the climate space is occupied by a given niche (see “range size” below). After thresholding, climate niches were rescaled to ensure that they integrated to one, which means that the volume under the two-dimensional climate space equals one for all estimated climate niches; this allows for estimation of overlap between any pair of climate niches (for further explanation, see below and Carmona et al., 2016). We used the package *TPD* (Carmona, 2019) to calculate the climate niches, following the procedures suggested by Broennimann et al. (2012) and Carmona et al. (2019).

We then estimated the dissimilarity between native and introduced niches for each species. For this, we used the overlap-based dissimilarity index, estimated as one minus the overlap between the native and introduced climate niches of each species (overlap being defined as the integral of the minimum of the two climatic niches; Carmona et al., 2016). This index reflects the extent to which the native and introduced climate niches of a species differ (Figure 2), ranging between zero (the native and climate niches are exactly distributed in the climate space) and one (when the two climate niches are completely disjoint) (Carmona et al., 2016; De Bello et al., 2013). We used the *dissim* function in *TPD* to estimate the dissimilarity between the climate niches in the native and introduced areas of distribution of 107 invasive woody legumes species. We considered the overlap classes suggested by Rödder and Engler (2011) to facilitate the interpretation of results: no or very limited overlap (0–.2), low overlap (.2–.4), moderate overlap (.4–.6), high overlap (.6–.8) and very high overlap (.8–1). Additionally, we explored the overlap using the niche availability method proposed by Broennimann et al. (2012); these results were very highly correlated with the overlap using the *TPD* package ( $R^2 = .96$ ; Supporting Information Figure S1). Because of this, and given that the *TPD* framework allows us to estimate other features of the patterns of occupation of the climatic space, we chose to report only *TPD*-based values. To ascertain whether the native and introduced niches of each species were less similar than expected by chance, we compared the observed overlap value with overlap values coming from a null model (Supporting Information Figure S2). The null model for each species consisted



**FIGURE 2** Illustration of the four climatic shift groups of invasive species, with the native distribution range depicted in blue and the introduced distribution range in red. Species were assigned to different groups according to the values of nestedness (Nest) and functional richness difference index [climate range size differences (Cdiff)] when comparing the native and introduced distributions. Both Nest and Cdiff values were evaluated against a null model that randomized the adscription of individual observations between the native and introduced ranges. Higher nestedness values than expected by chance ( $p$ -value for Nest  $> .9$ ) indicate that one of the climate ranges (either the introduced or the native) is contained within the other; in those cases, species were classified in the expansion group when the invaded climate niche was significantly larger than the native climate niche ( $p$ -value for Cdiff  $< .1$ ) and in the unfilling group when the native climate niche was significantly larger than the introduced one ( $p$ -value for Cdiff  $> .9$ ). In contrast, species with nestedness values lower than expected ( $p$ -value for Nest  $< .1$ ) were classified in the dissociation group, indicating that the two climate niches occupy at least some exclusive areas of the climate space. Finally, species whose nestedness value did not differ from that expected by chance ( $.1 < p$ -value for Nest  $< .9$ ) were included in the conserved group

of randomizing the native or introduced labels across all the observations of the species in the climatic space and estimating a new pair of niches (native and introduced), whose overlap was estimated as explained above (Traba et al., 2015). We repeated this procedure 999 times to achieve 999 null values for overlap. We then estimated the significance of the observed value of overlap by observing its rank within the simulated overlap values and estimated a two-tailed  $p$ -value from this ( $\alpha = .001$ ; Supporting Information Figure S2).

Additionally, we estimated the nestedness (Nest) component of the dissimilarity between the native and introduced niches of each

species. The nestedness component of dissimilarity expresses the proportion of the total dissimilarity between the two niches that comes from different patterns of occupation within the shared part of the functional space (Carmona et al., 2019; Figure 2). For example, if the invaded niche of a species is completely within the part of the climate space where the native niche is non-zero, the nestedness is equal to one. In contrast, if two niches are completely segregated in the climate space, the nestedness is equal to zero.

Finally, we estimated the total amount of climate space occupied by each niche (equivalent to the functional richness in the TPD

package) and subtracted the invaded range size from the native range size. This parameter, which we called climate range size difference (Cdiff), takes positive values when the native range occupies a larger part of the climate space than the introduced range and vice versa. Finally, we performed a null model to examine whether the proportion of space occupied in the introduced range was significantly higher or lower than in the native range (estimating a null distribution of Cdiff values through the same randomization procedure as in the overlap null model).

We used the results of the null models for Nest and Cdiff to characterize the patterns of occupation of the climate spaces between the native and introduced species ranges (Figure 2). Four different groups were defined (Supporting Information Table S3). First, the species in the conserved group were defined as those with similar occupation patterns between the native and introduced ranges. We included in this group those species whose nestedness value did not differ from that expected under the null model (i.e.,  $p$ -value for Nest between .1 and .9). Second, the expansion group included species with an introduced range that is larger than the native range and contains it. This means that the introduced range occupies the same climatic conditions as the native one, but also some new ones (Broennimann et al., 2012). We included in this group those species whose nestedness value was higher than expected under the null model ( $p$ -value for Nest > .9) and whose introduced niche was larger than expected by chance compared with the native range ( $p$ -value for Cdiff < .1). Third, the dissociation group included species with contrasting patterns of climate niche occupation between ranges (Fernández & Hamilton, 2015). We included in this group those species whose nestedness value was lower than expected under the null model ( $p$ -value for Nest < .1), indicating that both the native and introduced ranges occupy at least some exclusive portions of the climate space. Finally, the species in the fourth group, called the unfilling group, were those where the introduced niche occupies a subset of the native niche (i.e., the introduced range is nested within the native range). We included in this group those species whose nestedness value was higher than expected under the null model ( $p$ -value for Nest > .9) and whose introduced niche was smaller than expected by chance compared with the native range ( $p$ -value for Cdiff > .9).

Finally, we compared climatic shift groups (based on the differences between the native and introduced climate niches, as described in Figure 2) using mixed linear models, in which the first two axes of the PCA and all climate variables were considered as independent variables. We used species identity as a random factor to account for the repeated measures and the unevenness in the number of observations across species. Additionally, we used ANOVA to compare the values of the different functional traits between species groups.

### 3 | RESULTS

In general, native and introduced climate niches of the invasive woody legume species were highly dissimilar. Our results showed a

very limited overlap (.0–.2) between native and introduced distribution range for 20 species, low overlap (.2–.4) for 42 species, moderate overlap (.4–.6) for 38 species, high overlap (.6–.8) for only seven species, and no species showed very high overlap (.8–1.0) (Rödger & Engler, 2011). One hundred and three (of 107) presented significant differences between the native and introduced spaces (Figure 3; Supporting Information Figure S3). However, all species had at least some part of their introduced climatic space nested within their native range space (Supporting Information Figure S3).

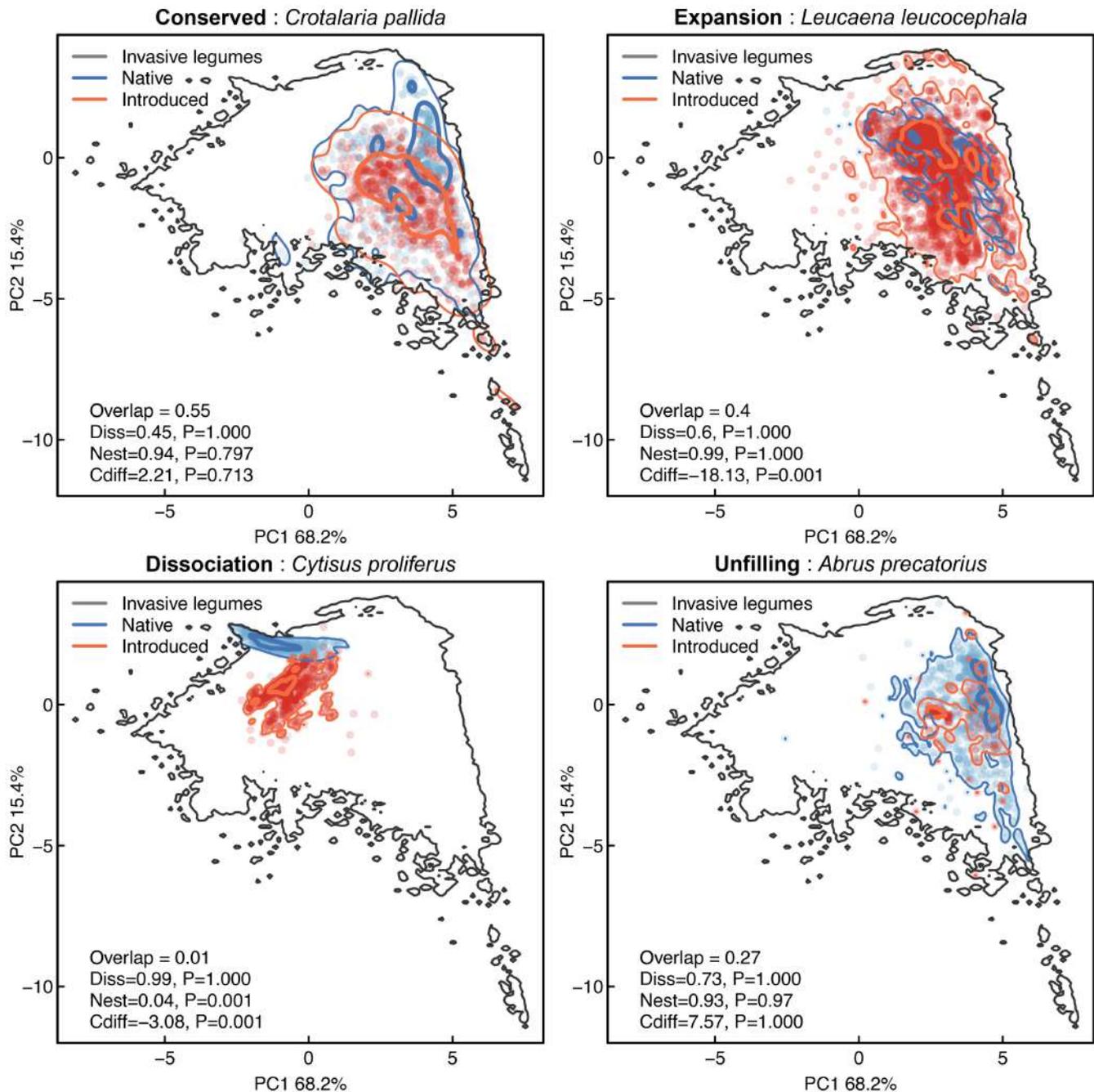
We defined four groups for invasive legumes according to the difference in occupation of the climate space between the native and introduced distribution ranges (Figure 3; Supporting Information Figure S3). Thirty species were classified in the conserved group, seven in the unfilling group, 21 in the expansion group and 49 in the dissociation group (Figure 3 includes examples of each group). Additionally, the  $\chi^2$  test showed differences in the frequency between the four groups ( $p < .001$ ), confirming that invasive woody legumes are disproportionately more likely to occupy the climate spaces in a different way from the native range.

There were significant differences between the climate space groups in PC1 (Figure 4), related to temperature. The species of the conserved group were primarily distributed at higher temperatures (high values in PC1) than the other groups. In contrast, we did not find significant differences between the groups in PC2 (Figure 4). Meanwhile, we found significant differences within groups (between the native and introduced ranges) in PC1 for all groups and in PC2 for conserved and expansion groups. The species of the conserved group presented significant differences between the native and introduced distribution ranges, with higher temperatures in the native range (Figure 4). The dissociation group showed the lowest temperature in the native range (Figure 4), increasing in temperature and decreasing in precipitation in the introduced areas (Supporting Information Figure S4). Also, this group did not show differences between native and introduced ranges in PC2 (Figure 4). Finally, both the unfilling and expansion groups showed higher temperatures in the native range than in the introduced range; however, the unfilling group invaded areas with higher precipitation than the native areas (higher values in PC2), whereas the expansion group pattern was the opposite (lower values in PC2 in invaded than in native areas) (Figure 4). Each group showed different behaviours regarding the individual climatic variables (Supporting Information Figure S4).

The only functional trait showing significant differences between groups of invasive species was leaf area. The main functional differences were found between the dissociation and expansion groups. Species in the expansion group had larger leaves (Figure 5a) than species in the dissociation group.

### 4 | DISCUSSION

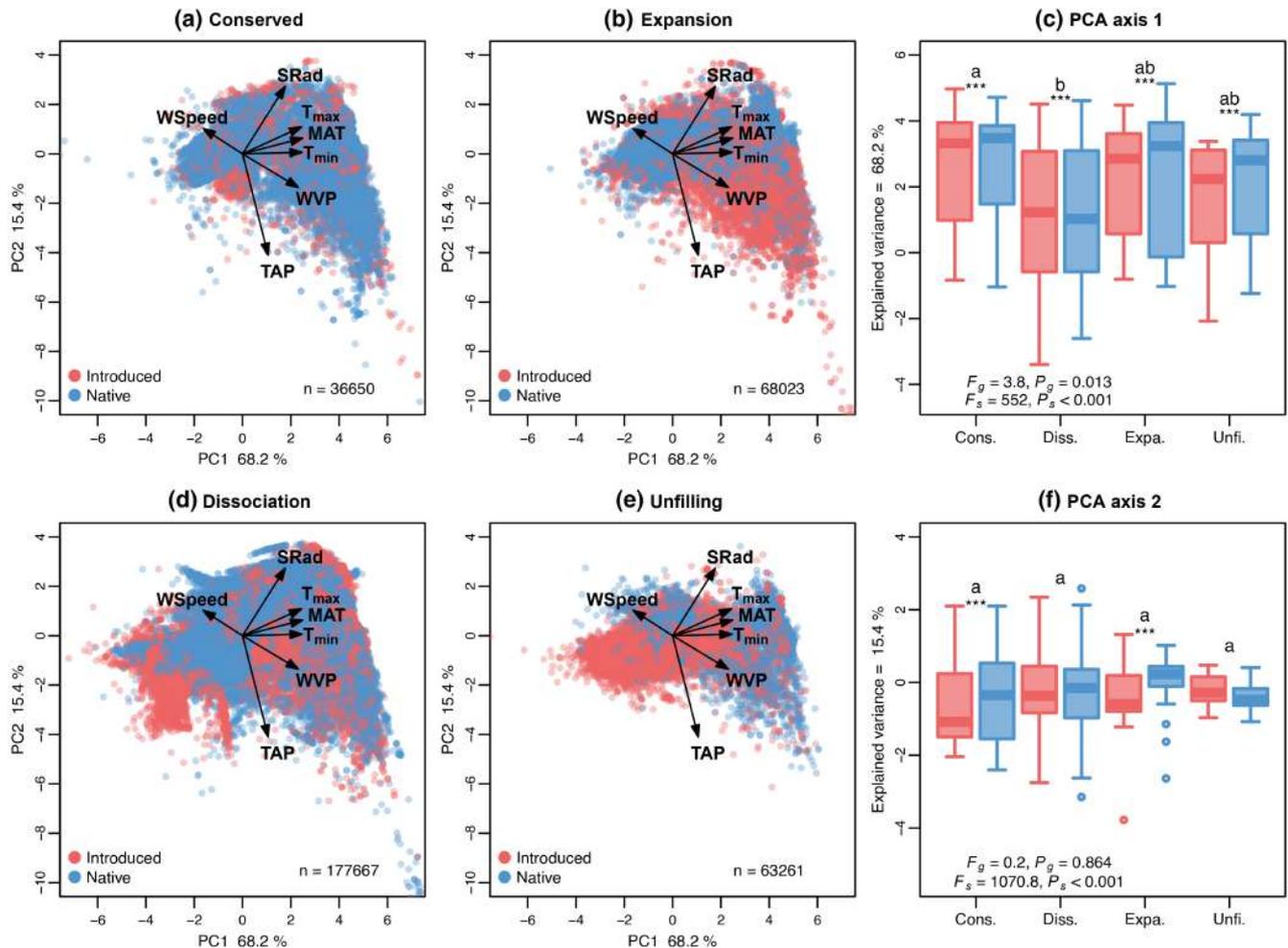
After comparing the climate of the native and introduced distribution ranges of 107 invasive woody legume species and how the differences between the two ranges in terms of climate might be driven



**FIGURE 3** Examples of species in the four groups according to their behaviour in the climatic space between native and introduced ranges (the climatic niches of the 107 studied species are available in Supporting Information Figure S3). For each species, blue and red dots depict native and introduced occurrences in the climate space, respectively. Lines show the 99 and 50% contour lines of the probabilistic distribution for each niche (native and introduced). Explanations regarding the criteria for including species in each group can be found in Figure 2 and in the main text

by functional traits, we found that invasive woody legume species generally exhibited low to moderate climatic overlap between their native and introduced distribution ranges, and these differences could be classified in four contrasting groups, of which an dissociation of the climatic space in the introduced range was the most common pattern, particularly in the case of species with little leaves. When we examined the different behaviours of the species concerning the occupied space, our results showed patterns consistent with

previous studies showing differences in climatic conditions between native and introduced areas (Broennimann et al., 2012; Early & Sax, 2014). However, our study had the advantage of including other indices that helped us to detect that low values of climatic overlap (high dissimilarity) do not necessarily indicate that the two distribution ranges do not share a large part of the climatic space. On the contrary, our nestedness analysis indicated that, in a majority of species, most dissimilarities in climate niches between the native and



**FIGURE 4** Differences in climate space by species groups. MAT = mean annual temperature; SRad = mean annual solar radiation; TAP = total annual precipitation;  $T_{\max}$  = maximum mean annual temperature;  $T_{\min}$  = minimum mean annual temperature; WSpeed = mean annual wind speed; WVP = mean annual water vapour pressure. The values of  $F_g$  and  $P_g$  indicate the results of the ANOVA by groups, whereas  $F_s$  and  $P_s$  indicate the results of the ANOVA by status for the groups (between native range and entered by group obtained from a mixed linear model). The letters indicate differences between the four groups of species and the differences between the native and introduced ranges for each of the groups in components 1 and 2, with the level of significance (\*\*<.001, \*\*<.01 and \*<.5)

introduced ranges are attributable to differential patterns of occupation of otherwise similar portions of the climate space (Supporting Information Figure S5). This result is consistent with the idea that environmental filtering influences the species distribution (Kraft et al., 2015; Rejmánek et al., 2005; Turner et al., 2015) and that the environmental conditions of the native area can predict the potential areas of invasion by the species (Early & Sax, 2014; Petitpierre et al., 2012). However, we recognize that other environmental factors, such as soil and mutualism characteristics, are an important part of the distribution of species, and including them in the future could help us to understand their distribution better (Beauregard & De Blois, 2014; Heikkinen et al., 2006; Simonsen et al., 2017).

Despite the generally high dissimilarity and high nestedness between native and introduced ranges, there were substantial differences among invasive woody legume species, which allowed us to classify them into four climatic shift groups. A majority of the legume species were classified in the dissociation group (49 species),

which included species with differences in climatic conditions between their native and introduced distribution ranges. The high prevalence of this group is in agreement with authors who have postulated that invasion success might be related to the ability of species to adapt to novel environmental conditions, having high climate tolerance (Perret et al., 2018). Nevertheless, 58 of the studied species exhibited a different behaviour, which makes it difficult to make broad generalizations. Likewise, it is possible that the climate space occupied by invasive woody legumes can change in space and time because of time elapsed since introduction and the future invasion advance in introduced areas (Beaumont et al., 2009; Gallagher et al., 2010).

Overall, we found significant differences in climate between the introduced and native ranges for all species groups, but with different directions. For example, the conserved group, despite showing high climate overlap, tends to occupy areas in the introduced range with lower temperatures and precipitation than in the native range.

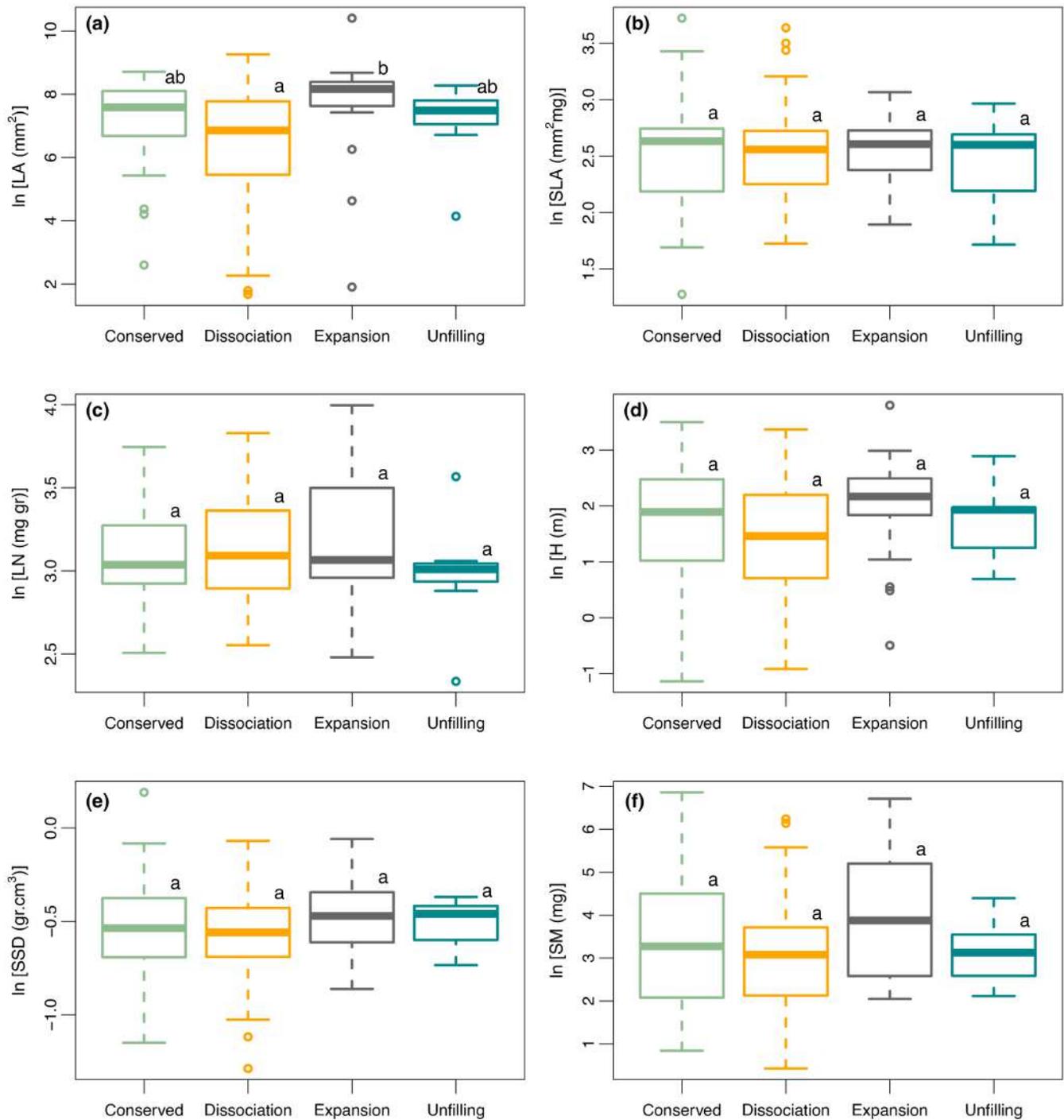


FIGURE 5 Differences in functional traits by species groups of woody invasive legumes. The lower case letters indicate differences between the groups of species obtained from the ANOVA by groups. H = plant height; LA = leaf area; LN = leaf nitrogen; SLA = specific leaf area; SM = seed mass; SSD = specific stem density

These species are already distributed naturally in climatic extremes, hence it is not surprising that they invade areas with less extreme climates (Hejda et al., 2015; te Beest et al., 2013; Turner et al., 2015). In contrast, the dissociation group, despite showing slightly higher temperatures in the introduced range than in the native distribution, is still the group with lower temperatures in the two distribution ranges. This suggests that the woody legumes of this group have a cold habitat preference and high climatic tolerance not expressed in

the native range (Araújo et al., 2013; Perret et al., 2018). Species in the expansion group expand beyond the edges of their native distribution preferentially by moving to introduced areas with lower temperatures and precipitation. This might be associated with abiotic restrictions (climate) in the introduced range and high climatic tolerance of these species (Araújo et al., 2013; Perret et al., 2018). Also, it is possible that species in the expansion group are either able to overcome or do not experience biotic restrictions when they find

new climates (Beaumont et al., 2009; Gallagher et al., 2010). The opposite happens with the species in the unfilling group (i.e., the introduced range is a subset of the native range in terms of temperature and precipitation). It is possible that the species in this group experience biotic or abiotic restrictions in the areas of introduction (Hejda et al., 2015; Turner et al., 2015), which reduce their realized climatic niche. Additionally, it is possible that many of these species have been introduced recently and, consequently, have not had time to express their full climatic niche in the areas of introduction (Bradley et al., 2014).

In terms of functional traits, our results showed that leaf area differed between species groups. These results are consistent with the expected relationships between functional traits and climate variables and contrast with the study by Gallagher et al. (2010), who found no differences in the functional traits between climatic shift groups. The conserved group presented high foliar area, which is consistent with its trend to occupy areas with high precipitation and temperatures (Wright et al., 2017). The expanded group presented the largest LA, and it is not distributed in extreme weather conditions, characteristics which generally describe acquisitive species (Funk & Vitousek, 2007; Leishman et al., 2007). Following the same logic, the unfilling group presented low LA, which is a common trait for species that are distributed in extreme climatic conditions, such as high temperatures (Bruehlheide et al., 2018). We also found low LA for species in the dissociation group, also associated with restrictive climatic conditions, such as lower minimum temperatures (Madani et al., 2018; Peppe et al., 2011). The functional traits of conserved and expanded groups are consistent with studies that describe invasive species as having acquisitive leaf traits (Carboni et al., 2017; Van Kleunen et al., 2010). Conversely, the functional traits of unfilling and dissociation groups were more conservative, which is typical in species that are able to tolerate extreme climatic conditions. For example, low LA reduces transpiration, reducing the risk of cavitation (Wright et al., 2017). We did not find differences between groups in the other traits considered, possibly because we considered only woody species from a single family, which restricts the amount of functional variation (Carmona, Bueno, et al., 2021). These results, along with other studies exploring the shift in the climatic space in combination with functional traits, are a very useful tool for understanding whether climatic distribution shifts in invasive species are a common component of the invasion process. Additionally, they can help to predict the future distribution of invasive plants, which is essential for anticipating and controlling invasions (Nunez-Mir et al., 2019; Qiao et al., 2017).

Overall, we can conclude the following three main trends. First, the studied species seem to show climate conservatism. However, the invasive woody legume species can distribute in new climatic conditions in the introduced area. Also, it would be interesting to include non-climatic factors, such as soil variables, mutualisms and disturbances that can complement the understanding of the distribution of invasive species in the invaded areas. Second, four different behaviours are possible between distribution ranges; however, the dissociation of the climatic niche in introduced areas is by far the

most common among woody legumes. These different behaviours might be the result of the time elapsed since introduction and adaptation to a new environment. In this case, monitoring the temporal changes in the climatic niche of these species would help us to gain a better understanding of the dynamics of the climatic niches associated with the invasion process. Third, the functional traits of the species groups are consistent with the expected patterns for their climatic distribution. In some species, climatic variables in the native distribution seem to be restricted to their distribution in the introduced range, which highlights the potential for using functional traits to predict the susceptibility of different environments to the invasion of a certain species. Combining information on the climatic niche and the functional traits of species appears to be an interesting tool to predict future invasions, both in climates similar to those of their native range and in new environments as a consequence of climate change.

#### AUTHOR CONTRIBUTIONS

All authors conceived the idea and led major contributions in the study. M.V.-V. wrote a first draft of the manuscript, and the other authors contributed to subsequent versions.

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#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

The authors declare that all occurrences of species were gathered from the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/>). Climate data were downloaded from WorldClim 2.0 - Global Climate Data (<http://www.worldclim.com/>). Coverage of invasive species was searched from the Invasive Species Compendium (CABI, <https://www.cabi.org/ISC>) and the International Legume Database and Information Service (ILDIS, <https://www.ildis.org/>). Legumes traits data was downloaded from publicly available data in TRY Plant Trait Database version 5.0 ([www.try-db.org/TryWeb/Home.php](http://www.try-db.org/TryWeb/Home.php)). The information on species classification, climate native, and introduced ranges are included in the Supporting Information S1. Additionally, a list of the references from which the data were extracted can be found in the Appendix.

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## SUPPORTING INFORMATION

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

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## APPENDIX

## Data sources

Affouard, A., Joly, A., Lombardo, J. C., Champ, J., Goeau, H. & Bonnet, P. (2020). Pl@ntNet automatically identified occurrences. v1.2. Pl@ntNet.

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