Niche dynamics of alien plant species in Mediterranean Europe

Cao Pinna[1,2], Luigi, Laure Gallien[3], Tommaso Jucker[4],Milan Chytrý[5], Greta La Bella[1], Alicia Acosta[1], Marta Carboni[1]

[1]Department of Science, Roma Tre University, Rome, Italy
[2]School of Mathematics and Statistics, University of Glasgow, Glasgow, United Kingdom
[3]University of Grenoble Alpes, CNRS, University Savoie Mont Blanc, LECA, Grenoble, France
[4]School of Biological Sciences, University of Bristol, Bristol, United Kingdom
[5]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

Abstract

Aim

Humans have spread plants globally for millennia, inadvertently causing ecological disruptions. However, biological invasions also provide a unique opportunity to study the process of niche dynamics, through which species adapt their niche when confronted with novel environments. Focusing on the Mediterranean Basin, we assessed 1) which traits favour niche dynamics, and 2) whether niche conservatism or niche shift promotes invasion success.

Location

Mediterranean Europe and the World.

Methods

We selected the 85 most widespread alien vascular plants in Mediterranean Europe and compiled data on their distribution in their native and invaded ranges. We then tested how a species' residence time, biogeographic origin, dispersal ability, functional traits and intraspecific trait variability (ITV) influence its niche dynamics following invasion. Using already published independent data, we finally assessed whether niche dynamics can explain different dimensions of invasion success (such as regional spread or local abundance).

Results

We found that niche shifts were common (71% of species) and were mostly driven by species failing to occupy all suitable environments of their invaded range (unfilling), regardless of residence time. Niche unfilling and niche expansion were more important in species with high intraspecific trait variability introduced from non-mediterranean biomes (temperate or tropical). Niche expansion was also greater in species with long-distance dispersal, bigger seeds and a narrow native niche. Interestingly, invasion success correlated more with a species' ability to conserve its niche and residence time than with niche expansion.

Main conclusions

Niche shifts were better predicted by species traits than residence time. For example, high adaptive potential (inferred from high intraspecific trait variability) favoured niche shifts in general, and long-distance dispersal favoured niche expansion. Understanding how these traits relate to niche dynamics is important since a species' ability to conserve and fill its niche is in turn a good predictor of invasion success.

Introduction

People have been moving plants around for millennia, often with unexpected and ecologically disastrous consequences (Pyšek et al., 2020; van Kleunen et al., 2015). But this process of reshuffling floras also presents an opportunity to study niche dynamics, the process through which species adapt their niche when confronted with a novel ecological setting (Atwater, Ervine, & Barney, 2018; Colautti & Lau, 2015). A central tenet of niche theory has been that species largely conserve their niches on short ("ecological") timeframes (i.e., niche conservatism, Wiens et al., 2010) and tend to occupy similar environments when introduced into new areas (Petitpierre et al., 2012; Strubbe, Broennimann, Chiron, & Matthysen, 2013). However, many recent invasion studies have challenged this view, reporting cases of alien species that have considerably shifted their realised niche following invasion (Atwater & Barney, 2021; Atwater et al., 2018; Broennimann et al., 2012; Early & Sax, 2014). Studies examining these rapid niche shifts have yielded contrasting results, with some studies showing them to be common (Dellinger et al., 2016; Liu, Wolter, Xian, & Jeschke, 2020) and others concluding shifts to be rare (Liu, Wolter, Xian, & Jeschke, 2020; Petitpierre et al., 2012; Sychrová, Divíšek, Chytrý, & Pyšek, 2022). These inconsistencies are partly attributable to methodological differences across studies (Bates & Bertelsmeier, 2021; Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014), but also to the dependence of niche shifts on the ecological characteristics of the species itself (e.g., Dellinger et al., 2016; Li, Liu, Li, Petitpierre, & Guisan, 2014; MacLean & Beissinger, 2017). Identifying which species are most likely to shift their realised niche is particularly relevant if this ability can contribute to the invasion success in new environments (Sotka et al., 2018; van Kleunen, Weber, & Fischer, 2010). However, the ecological characteristics favouring niche shifting and the link between niche dynamics and invasion success are poorly understood.

Niche dynamics, resulting in either niche conservatism or niche shifts, can be assessed by comparing species' niches based on environmental data and occurrence records in their native and invaded ranges (Di Cola et al., 2017). The most robust framework currently available to quantify and statistically test for niche shifts in environmental space restricts this comparison to the shared, analogue environmental conditions between the native and invaded ranges (Guisan et al., 2014) because the colonisation of environments not available in the native range cannot unambiguously be ascribed to niche evolution. According to this framework, when colonising a new region, invasive species can either maintain, expand, or fail to fill their native niche (Pearman, Guisan, Broennimann, & Randin, 2008). The realised niche quantified in the invaded range can thus be divided into three parts: (i) niche stability, the part of the niche that the species occupies in both its native and invaded ranges; (ii) niche expansion, the portion of environmental space occupied exclusively in the invaded range; and (iii) niche unfilling, the set of environmental conditions occupied only in its native range.

Niche unfilling may be a consequence of dispersal limitation in the invaded range (e.g., dispersal barriers or poor dispersal ability; Giulio et al., 2022; Li et al., 2014), but may also occur if positive interactions have been lost during invasion (e.g. if mycorrhiza or other mutualists have not been introduced at the same time; Grove, Haubensak, Gehring, & Parker, 2017; Menzel et al., 2017). Conversely, niche expansion may occur if species evolve novel local adaptations that allow them to spread outside the limits of the environmental conditions occupied at home (Bujan et al., 2021; Lancaster, Dudaniec, Hansson, & Svensson, 2015) but also if dispersal barriers are limiting their native range (Bates & Bertelsmeier, 2021) or if enemy release and new facilitations occur in the new range (Keane & Crawley, 2002). In sum, dispersal limitation, biotic interactions and local adaptations are the main processes that are likely to influence niche dynamics in the invaded range, and species ecological characteristics related to these processes may help explain variability across taxa.

Dispersal limitations play a major role in the spatial patterns of invasive species. These limitations are the result of a combination of factors, including species-specific introduction history and dispersal abilities. Introduction history is particularly relevant as it relates to the likelihood of overcoming landscape barriers in the invaded range. Species with the intrinsic ability to disperse over great distances are less likely to have been dispersal limited at home (and thus less likely to expand their niche after introduction) but also in the invaded range (i.e., more likely to rapidly fill their niche once introduced). Recently introduced species with poor dispersal ability may thus not yet have reached all the environmental conditions they occupy in their native range (stage of unfilling). In contrast, species introduced longer ago with good dispersal ability will have had more time to overcome barriers and fill or potentially expand their niche (Li et al., 2014). Consequently, both residence time and species dispersal ability could influence niche unfilling and expansion (Menuz, Kettenring, Hawkins, & Cutler, 2015).

Biotic interactions are also well known to be crucial in the invasion success of introduced species. Enemy release in the invaded range (i.e., the loss of predators, parasites and competitors, Brian & Catford 2023; Keane & Crawley, 2002) can lead to an expansion of the realised niche in new environments free of native antagonists. Species with traits typically associated with slow resource acquisition, such as short stature, slow growth and big seeds (e.g., Gioria et al., 2023; Richardson & Pyšek, 2006; van Kleunen, Weber & Fischer, 2010), are poor competitors in disturbed areas and may be more likely to expand their niche when they are released from their antagonists that otherwise limit their establishment. In contrast, plant species that are highly competitive in resource acquisition at home (e.g., high SLA) might be relatively unaffected by release from competitors, especially in disturbed habitats. However, these fast-growing plants often have low investment in defences against herbivores (e.g., high SLA often means high palatability, de Vries, Evers, Dicke, & Poelman, 2019), so they might instead experience greater release from predators or parasites, resulting in niche expansion and potentially better niche filling (Bates & Bertelsmeier, 2021). In addition to plant traits, the environmental context in which a species evolved, like its biome of origin (Mucina, 2019; Olson et al., 2001), might also be important for explaining niche dynamics (e.g., if the new range hosts similar mutualists and/or antagonists because it shares the same bioclimatic conditions as the species' native range; Cao Pinna et al., 2021). Similarly, species with broad realised niches at home are less likely to be constrained by dispersal barriers or biotic interactions and are more likely to occupy suitable environments in novel areas with less expansion and less unfilling (Mitchell & Power, 2003). These species would not find many additional environments to expand their niche compared to species with narrow environmental tolerances (Bates et al., 2020; Gallien, Thornhill, Zurell, Miller, & Richardson, 2019; Early & Sax, 2014). Thus species' ecological characteristics, bioclimatic pre-adaptations and native niche breadth can potentially predict expansion and unfilling. However, despite this strong theoretical underpinning, the effects of species traits and biogeography on niche dynamics have only been explored by a handful of studies (Bates & Bertelsmeier, 2021; Li et al., 2014).

Finally, while changes in dispersal limitations and biotic interactions will mainly affect a species' realised niche, rapid evolution and local adaptation in response to novel conditions may also result in shifts in its fundamental niche. These processes may play an important role in driving niche dynamics following the invasion, given that several invasive species have been found to have rapidly evolved in their new ranges as a result of increased genetic variation, interspecific hybridisation, genetic bottlenecks, or natural selection in novel environments (Bock et al., 2021; Gallien et al., 2016; Colautti & Barrett, 2013). For instance, Dellinger et al. (2016) hypothesised that sexually reproducing plants should be more likely to shift their niches following invasion due to their higher genetic diversity. However, the reproductive system is only one proxy of genetic diversity (Colautti & Lau, 2015; Smith et al., 2020), and other characteristics may be associated with greater evolutionary flexibility (Bujan et al., 2021; Lancaster et al., 2015). For example, intraspecific variation in functional traits (ITV) reflects a combination of phenotypic plasticity and heritable genetic variation (Karbstein, Prinz, Hellwig, & Römermann, 2020). Consequently, we might expect that higher ITV should be related to greater evolutionary and adaptive potential (Davidson, Jennions & Nicotra, 2011; Karbstein et al., 2020) and theoretically also to a greater potential for niche shifts during invasions. Yet, the relationship between species' ITV and their niche dynamics remains to be tested.

To test these ideas, we compiled distribution and trait data for the most widespread alien plants in Mediterranean Europe. We focused on the Mediterranean Basin, one of the world's biodiversity hotspots (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011), because it has a long history of human exploitation that has led to the introduction of numerous alien plant species (Underwood, Viers, Klausmeyer, Cox, & Shaw, 2009). This makes the Mediterranean Basin an ideal arena to study the niche dynamics of introduced alien plants, as within one biogeographically and climatically defined region we can compare a large number of species with contrasting introduction histories, dispersal abilities and functional traits. Using this unique dataset, we quantified niche shifts by comparing alien species' niches in Mediterranean Europe with their niches at home and tested whether these shifts are underlain by expansion and/or unfilling. Then we tested the following overarching questions:

1) Is niche shift common in invaders of Mediterranean Europe?
2) Which are the ecological characteristics that limit niche filling and favour expansion?
3) Is invasion success in Mediterranean Europe more frequent in niche-shifting species or in species that conserve their niche?

Material and Methods

Study area and alien species records

To quantify niche shifts in plant species introduced to Mediterranean Europe (including Anatolia and Cyprus), we first identified the most widespread alien plants in the study area and then quantified their native and invaded niche using a combination of presence records and data on their bioclimatic envelope. The invaded range included the Mediterranean biogeographic region in Portugal, Spain, France, Monaco, Italy, Malta, Croatia, Bosnia and Herzegovina, Montenegro, Albania, Greece, Turkey, and Cyprus, as defined by the European Environmental Agency (EEA; Cao Pinna et al., 2021). We focused on alien plants reported in vegetation surveys throughout the study area, as identified by Cao Pinna et al. (2021), and selected the 100 most widespread and abundant neophytes (i.e., species introduced after 1500 AD) identified in Cao Pinna et al. (2024). For these neophytes, we extracted the global occurrences from the Global Biodiversity Information Facility (GBIF; accessed in 2020). We excluded GBIF records older than 1950 and with a reported location uncertainty >5 km. We post-processed the data (R package 'CoordinateCleaner'; Zizka et al., 2019) to remove occurrences 1) with clearly erroneous coordinates (e.g., falling in the sea or with equal longitude and latitude) or 2) within 1 km from biodiversity institutions (botanical gardens, herbaria, universities, and museums), country centroids and GBIF headquarters. We also retrieved the native range reported for each species from the database of Plants of the World Online (POWO, https://powo.science.kew.org/, accessed 2022). We then removed species with less than 8 presences at 1 km resolution in the native range following the suggestion by Broennimann et al. (2012) of the minimum sample size required for niche shift analyses. After the processing, we were left with 85 species, with a mean of 1861 presences in the invaded range (min = 34, max = 7700) and 1184 presences in the native range (min = 8, max = 22300).

We complemented the presence database by sampling background environments for each species in both the native and the invaded range. We constrained the background sampled environmental conditions within a buffer area of 100 km around each species' presence in the native and invaded range, to select only areas potentially reachable by each species. We compared alternative buffer sizes (Supporting S1.1) and retained 100 km because a smaller buffer is unrealistic, while a bigger one did not significantly change niche shift dynamics results (sensitivity test shown in S1.1).

To estimate the environmental conditions that species occupy in their native and invaded ranges, we selected five variables that jointly capture the environment in the Mediterranean Basin (Deitch, Sapundjieff, & Feirer, 2017), including one related to soils, which is often overlooked (Liu, Wolter, Xian, & Jeschke, 2020). These variables included: the annual temperature range (bio-07), mean temperature of the warmest quarter (bio-10), precipitation of the wettest quarter (bio-16) and precipitation of the driest quarter (bio-17), which we obtained from the CHELSA database at approximately 1 km resolution (Karger et al., 2017), as well as soil bulk density from the SoilGrids database (250 m resolution, Hengl et al., 2017). In choosing these variables, we also avoided those strongly correlated with one another (excluding those with a Pearson correlation coefficient > 0.7 for all pairwise comparisons). Finally, all environmental layers, species presences and background points were resampled at 1 km resolution to avoid spatial mismatch between datasets.

Quantifying niche dynamics

For each of the 85 study species, we quantified niche shifts that occurred following their introduction in Mediterranean Europe. First, the background environmental variables (native and invaded ranges together) were summarised using a Principal Component Analysis (PCA) and then rescaled to an environmental grid (100x100 cells) using a kernel smoother to estimate densities (Broennimann et al., 2012, package 'ecospat' version 3.2, Di Cola et al., 2017). This allowed us to directly compare the native and invaded niches using the first two axes of the PCA that captured 73 ± 4 % of the total variance in the environmental space on average across species, while also partially controlling for sampling and environmental biases. We determined the overlap of the occurrence densities in the environmental space by estimating Schoener's D (Schoener, 1970), which ranges between 0 (no overlap) and 1 (complete overlap). To test if the native niche is more similar than expected to the invaded one, we compared the observed D value with those obtained from 1000 random invasive niches (i.e., testing if the observed overlap is higher than 95% of simulated niches). For each species, we used the observed and random D scores to (1) determine if it has shifted its niche or not (p-value threshold of 0.05), and (2) quantify nice shift strength (measured as 1-D).

We further decomposed niche dynamics into expansion and unfilling focusing on the analogous environmental space. Niche expansion was measured as the percentage of the niche in the invaded range which is not occupied in the native range (and represents along with stability, 100% of the invaded niche). Niche unfilling was measured as the percentage of the native niche not occupied in the invaded range.

Identifying the ecological characteristics that drive niche shifts

We tested whether: (i) residence time, (ii) species dispersal ability, (iii) biogeographic origin, (iv) native environmental niche breadth, (v) functional traits or (vi) their variability (i.e., ITV or species plasticity) were good predictors of niche expansion and unfilling. We quantified residence time as the number of years since the first record in any of the countries of our study area, using the freely available database from Seebens et al. (2017). The maximum dispersal distance for each species was defined following the approach proposed by Tamme et al. (2014) using the R package "dispeRsal" using dispersal syndrome, growth form, seed mass and plant height as predictors (all obtained from the TRY database; Kattge et al., 2020). As an indicator of biogeographic origin, we used the biome of origin from Cao Pinna et al. (2021), and aggregated species into three broad bio-climatic categories: temperate, tropical and Mediterranean/xeric. We defined the degree of native environmental niche breadth as the size of the multivariate environmental space occupied by each species in its native range using a minimum convex polygon (i.e., convex hull using the R package "adehabitatHR"). In terms of functional traits, we chose those that jointly describe a species' competitive ability: specific leaf area (SLA), plant height, seed mass, growth form (i.e., herbs, shrubs, trees), and life span (i.e., perennial/annual). SLA relates to the ability to capture resources rapidly (i.e., higher SLA values reflect faster growth rates), plant height captures the ability to compete for light in the adult stage, seed mass is related to growth rate and competitive ability in the seedling stage and to dispersal (Gioria et al., 2023), while growth form and life span provide a more integrated view of a species' competitive strategy. We obtained values for these traits from the TRY database, and for the three continuous traits, we calculated an average trait value for each species. To estimate the degree of ITV in the three continuous traits, we calculated the coefficient of variation across all available records for each species (ITV was not related to sample size - Supporting Information S.2 for each species data).

We used multiple regression models with a beta distribution (specific for percentages - using the R package "glmmTMB") to test the influence of these drivers on the percentages of i) niche expansion and (ii) unfilling. Stepwise variable selection based on Akaike's Information Criterion (AIC) was used to simplify the models. Moreover, given the complexity of the variable structure, we complemented the model selection process with a Random Forest (R package "randomForest") and Multimodel Inference (R package "MuMIn") to assess the consistency of variable selection between modelling choices (showing high agreement among model selection techniques, see Supporting Information S1.2). Given that closely related species may be non-independent, we also tested for phylogenetic signals in our niche shift metrics. To do so, we first built a custom phylogeny for our species, based on the backbone phylogeny of vascular plants (Smith & Brown 2018), and then we calculated Blomberg's K (Blomberg, Garland, & Ives, 2003) and Pagel's lambda (Pagel, 1999) indices for our two niche shift metrics of unfilling and expansion (Supporting Information S1.3). As we found a lower phylogenetic signal than expected by chance for all metrics, we did not account for species phylogenetic relatedness in our models.

Linking niche shift to invasion success

We tested whether shifting the niche gave an advantage in different invasion success components, taking into account the confounding effect of residence time. To characterise the invasion success of each species in Mediterranean Europe, we used the results of Cao Pinna et al. (2021), who analysed 130,000 vegetation plots from the European Vegetation Archive (EVA; Chytrý et al., 2016). From these, they calculated each species' commonness in terms of its: invaded range size (i.e., the geographic regional spread) and local abundance (i.e., the mean cover across plots where it occurs, see Cao Pinna et al., 2021). We used structural equation modelling (R package “piecewiseSEM”), and multiple linear regression analysis (except for niche shift - where we applied a binomial logistic regression model) to investigate the direct and indirect drivers of non-native species’ regional spread and local abundance. Specifically, we tested 1) the effect of residence time on niche shift (binary variable consisting of two levels, "shifted" or "not shifted") and on niche expansion, and 2) the direct and indirect effects of residence time, niche shift and expansion on the regional spread and local abundance (Fig. 3). Even though niche shift comprises both expansion and unfilling, we specifically tested the role of niche expansion for invasion success as it is generally associated with processes favouring invasion success, e.g., local adaptations or enemy release. We did not test unfilling because of its high association with niche shift strength (Spearman's rank correlation rho = -0.75). The global goodness-of-fit of the SEM was evaluated via Fisher’s C statistic ($p > 0.05$). Again, we ruled out the need to account for phylogeny in the analyses (Supporting Information S1.3).

Results

Is niche shift common in Mediterranean Europe?

We observed that niche shifts were common across the 85 most widespread alien plant species in Mediterranean Europe, with 60 species (71%) occupying environments significantly different from those in their native range (Fig. 1a and b for niche shift strength). These shifts were mainly due to unfilling, with (42+16)/60 species (Fig. 1c) experiencing at least 10% of unfilling (average = 44%). By contrast, niche expansion was much rarer, with only 16/60 species showing at least 10% expansion (average = 12%, Fig. 1c and d).

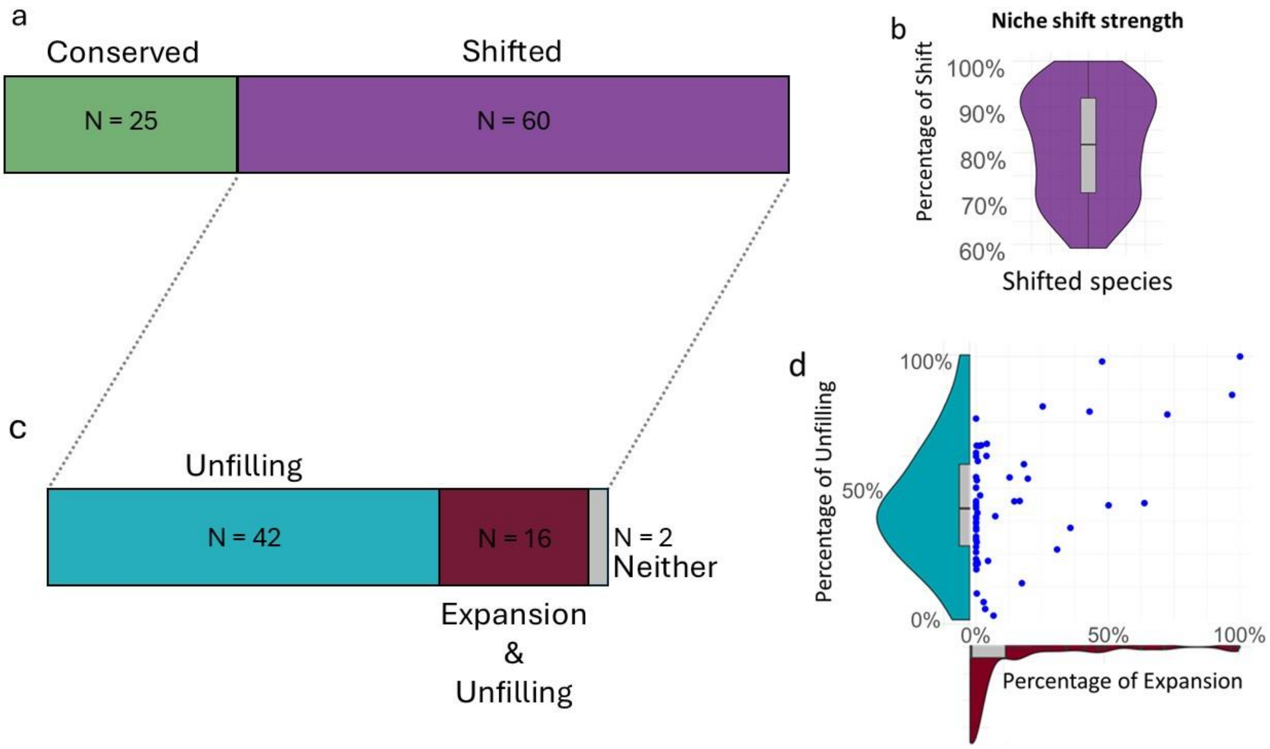

Figure 1: Bar plots showing the number of species that conserved or shifted their niche (a). Violin plot, with the niche shift strength for all niche shifting species identified in Mediterranean Europe (b). Barplots, showing the number of species that shifted their niche and had more than 10% expansion or unfilling (c, 2 species had neither more than 10% expansion nor unfilling in the shared environmental space - but still shifted their niches, for example when they have little overlaps in the environmental space). Violin charts combined with a scatter plot show the strength of expansion and unfilling for the niche-shifting species (d).

Which ecological characteristics favour niche niche expansion or unfilling?

Our best beta regression models for expansion and unfilling could explain 52% and 28% of the variance respectively. Niche expansion was found to be higher in species with high dispersal distance, with high mean SLA and seed mass, and high seed mass variability, in annual species, and those introduced from temperate and tropical biomes (ϕ = 5.6; p < 0.0001, R^2 = 0.52, d.f. = 10; Fig. 2a and c for specific examples). In contrast, it significantly decreased with native niche breadth. We found that the degree of unfilling significantly increased with mean SLA, species trait variability (in seed mass) and for some biomes of origin (temperate and tropical, compared to the Mediterranean; ϕ = 5.3; p < 0.0001, R^2 = 0.28, d.f. = 6; Fig. 2b,c and d for specific examples). Residence time, as well as the other tested variables, such as plant height, growth form and ITV for some traits - although potentially relevant, were not significant for these final models.

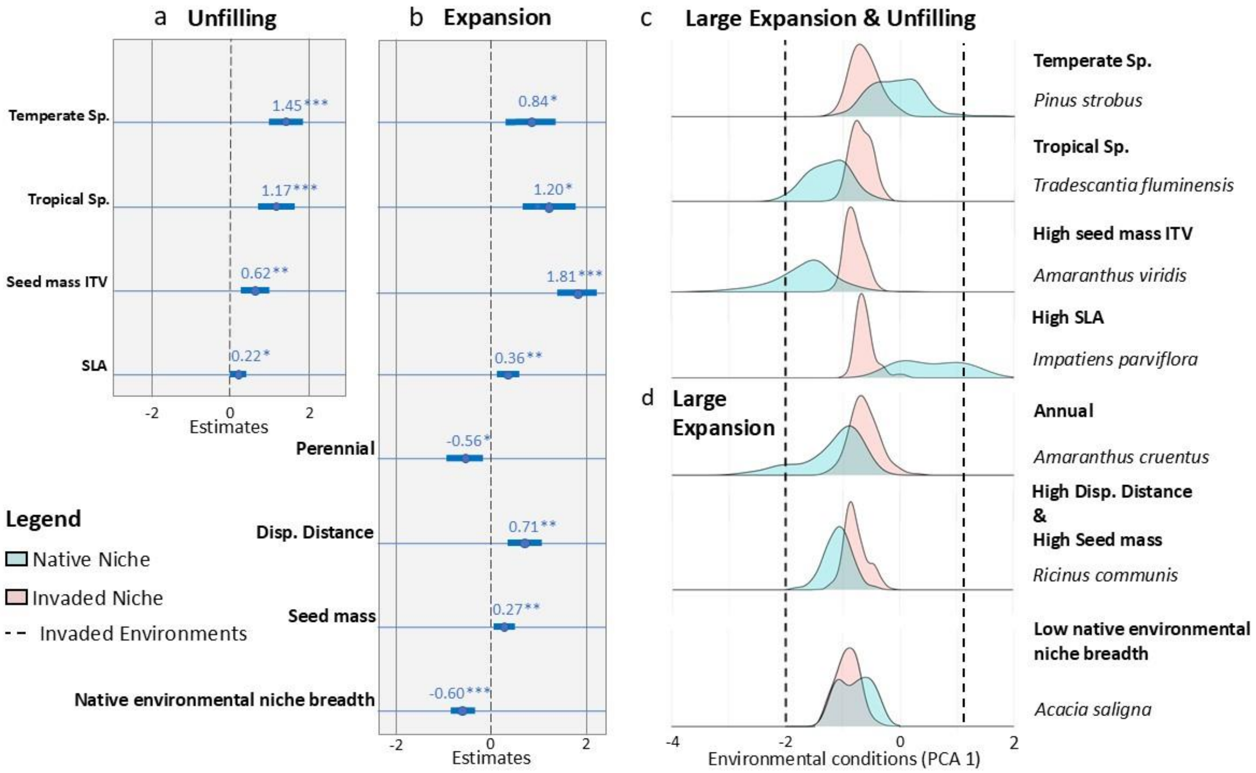

Figure 2: Importance of invader ecological features in niche dynamics. Standardised estimates (± Std. Error) for each significant predictor (after model selection) of the multiple beta regression for (a) the best model for explaining the level of niche unfilling and (b) the best model for explaining niche expansion. Blue bars represent a statistically significant relation (with an asterisk for the significance values). Estimated values for the categorical variables are compared to Mediterranean/xeric species for the biomes of origin, and compared to "annual" for the life span. (c and d) Illustration of individual species niche comparison between the native (blue) and invaded range (red), presented on the first axis of a PCA calibrated using the global environmental conditions (for better comparison among all species). Sampled species are illustrative examples of how species characteristics influence realised niche dynamics. Legend: * p-value < 0.05, ** p-value < 0.01 and *** p-value < 0.001.

Is invasion success in Mediterranean Europe more frequent in niche-shifting species or in species that conserve their niche?

Our structural equation model (Fisher's C = 6.5, d.f. = 4, p = 0.16) showed only the direct effects of residence time and niche shift on invasion success but not an interplay between them or niche expansion. We found that a species' ability to conserve its native niche, rather than shifting it, favoured invasion success in Mediterranean Europe (Fig. 3). Specifically, we found that residence time had no effect on niche shift, and species that conserved their niches ("not shifted" as a binary output) were more regionally widespread in the invaded range (std. estimate = -0.25; df = 81; p = 0.03; Fig. 3). Conversely, niche shifting or conservatism did not influence significantly local abundance in the invaded range (std. estimate = -0.05; df = 81; p = 0.64; Fig. 3) while residence time did (std. estimate = -0.34; df = 81; p = 0.002; Fig. 3).

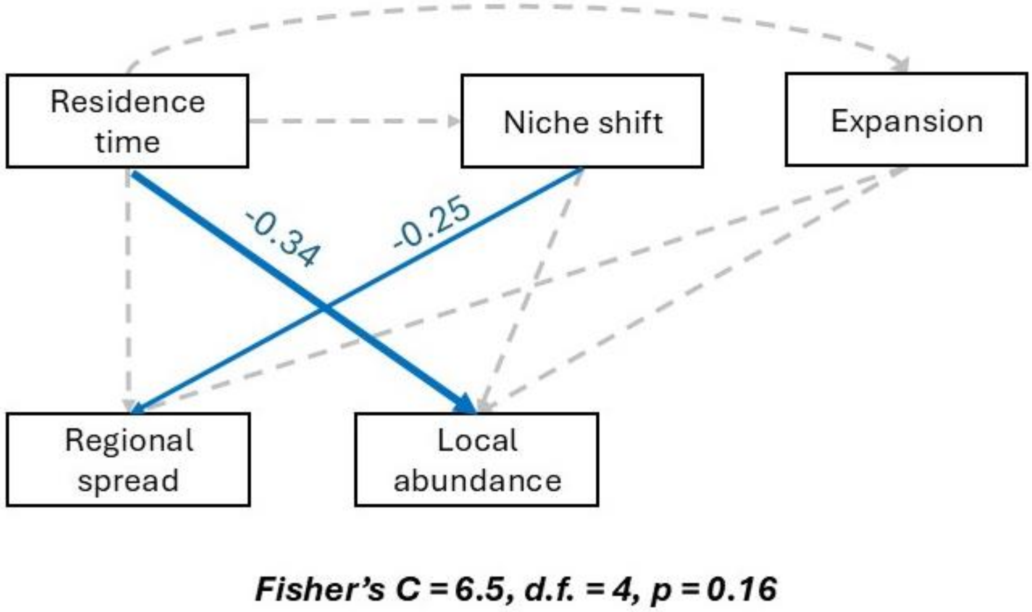

Figure 3: Results of the structural equation model used to test the direct single effect of residence time on niche shift (used as a binary variable: "shifted the niche" or "not shifted") and expansion. The model was also used to test the combined effect of residence time, niche shift and expansion on the two facets of invasion success: local abundance and regional spread. Blue arrows represent significant relations (the arrow's size refers to the std. estimate intensity, i.e. the value on the arrows), and grey dashed lines refer to the tested but not significant relations.

Discussion

Realised niche shifts are common in Mediterranean Europe

Our results show that most of the alien plants introduced in Mediterranean Europe occupy environmental conditions that are different from those in their native range: realised niche shifts are common in this area. Most of these species shifted their niche primarily because of their inability to fill the environmental conditions already occupied in their native range (i.e., unfilling) rather than because of niche expansion, (Atwater et al., 2018; Bates et al., 2020; MacLean & Beissinger, 2017; Strubbe et al., 2013), although the two values were slightly correlated (Fig. 1d).

Compared to earlier studies on alien plants, our results show more frequent niche unfilling and less frequent niche expansion (e.g. Sychrová et al. 2022 for introduced trees and shrubs, González-Moreno et al. 2015 for introduced O*xalis*). These differences with other studies may be due in part to the use of an additional edaphic variable to estimate species niches, in addition to climatic variables. This increases the number of dimensions of the niche space and makes it more likely to observe unfilling patterns (e.g. when species are constrained by unfavourable edaphic conditions). Second, compared to previous studies, we also analysed herbaceous growth forms, and therophytes in particular are well known for having many ecological differences from woody plants (e.g., spending part of their life cycle as seeds and having different tolerance to stress), potentially causing more unfilling and less frequent expansion in our results. However, these particularly low levels of expansion in niche shifts have been found in other studies on single species like in Dinis et al. (2020), and may also be linked to the harsh environmental and biotic filters combination of the Mediterranean climate.

Niche dynamics are extensively explained by dispersal limitation, biotic interactions and local adaptations

Like several previous authors, we found that residence time did not influence species niche dynamics (Dellinger et al., 206; Early & Sax, 2014; Petitpierre et al., 2012). In a region with long human exploitation such as Mediterranean Europe, processes more complex than just time for dispersal may be at play, and species ecological characteristics were better predictors of both niche unfilling and niche expansion.

For example, we found that the intrinsic dispersal ability of the species favours niche expansion. One potential explanation is that most alien species were limited in their native range by extrinsic barriers that could not be overcome naturally, irrespective of their dispersal ability. Only in the invaded range and thanks to the human-mediated introductions, their natural dispersal ability becomes an important factor favouring expansion in novel climates (Bates et al., 2020; Menuz et al., 2015; Smith et al., 2020). This interpretation is also congruent with the finding that species with broad native environmental niche tolerance have minimal expansion in the analogue environments since they are typically not dispersal-limited in their native range (Bates & Bertelsmeier, 2021; Early & Sax, 2014). Moreover, this result is in line with other studies (e.g., Bates et al. 2020; Dellinger et al., 2016) finding that species with a narrow native niche tend to have more expansion because they could benefit more from human-mediated dispersal, allowing them to access novel climatic conditions of their fundamental niche.

Our results are also consistent with the idea that niche shift dynamics are influenced by the novel biotic interactions established in the invaded range, supporting the importance of enemy release and maintaining positive mutualistic interactions. We found that species with large seeds, which are theoretically poor competitors at the seedling stage, slow growers and poor invaders (as they generally also have small seed production; see e.g. Gioria et al. 2023), were more likely to expand their niche after being released from their native range competitors and enemies (Brian & Catford 2023). Nevertheless, we also found that species with high SLA tended to expand their niche, despite being fast in resource acquisition and hence competitive species in disturbed environments, which are theoretically not strongly limited at home. However, these fast-growing species are likely the ones with the least investment in defences from enemies (de Vries, Evers, Dicke, & Poelman, 2019, Brian & Catford 2023). Thus, once freed from pathogens, herbivores and competitors of their native range, their high competitive ability may favour the expansion of their niche (Mitchell & Power 2003; Brian & Catford 2023). Another interesting novel result is that climatically pre-adapted species from other Mediterranean/xeric biomes have less expansion in the invaded range than temperate and tropical species. Species of Mediterranean/xeric origin may find ecologically similar competitors and herbivores (“analogous” enemies) in the invaded range, resulting in limited enemy release and less expansion (for example according to this framework; Brian & Catford 2023). Similarly, these climatically pre-adapted Mediterranean/xeric species coming from comparable environmental conditions, may find mutualist species in the invaded region (Mucina, 2019; Olson et al., 2001). This may allow them to conserve some of the positive ecological interactions already established in their native range, favouring niche filling, if compared with temperate and tropical species, as we found in our analysis.

Finally, we found that species with greater ITV in some traits (specifically in seed mass; Violle, Castro, Richarte & Navas, 2009), as an indicator of evolutionary and adaptive potential, were subject to more niche expansion, as we predicted. Species with more variable seeds may be able to expand better in novel environments because of their greater evolutionary and adaptive potential in the early stages of invasion. Indeed it has been shown that local adaptation can evolve quickly during range expansion in invading plants (Colautti & Barrett, 2013). Specifically, species with more variable seeds (rather than with more variable SLA or height) may be advantaged in a wider range of environments because of their higher persistence in the soil seed bank and establishment ability (Gioria et al., 2023, Gioria et al., 2021). Surprisingly, we found that ITV in seed mass did not just favour niche expansion into novel environments but was also associated with greater unfilling. Brian & Catford (2023) proposed genetic bottlenecks as a potential explanation for the limited ability of species to fill their niche when low genetic diversity is introduced in the invaded range. Species with high ITV globally may also be more prone to experience genetic bottlenecks in the invaded range, given that often only a small subset of their genetic diversity is introduced. Thus, while ITV can be an indicator of high adaptive potential favouring expansion it may also be associated with bottlenecks that could lead to unfilling. However, we appreciate that we measured ITV at the global scale and do not know the true genetic variability introduced in the invaded range, nor whether observed niche shifts are truly adaptive. Thus interpretations of this specific result should be carefully evaluated and further tested in future research (e.g. addressing if niche expansion has been enabled by genetic changes adapting the species to new environments), also given that out of the three traits tested, only seed mass showed a significant trend for ITV.

Niche conservatism in the invaded range explains invasion success

Contrary to the expectation that rapid local adaptation is one of the reasons why alien species become invasive (e.g., Bujan et al., 2021; Sotka et al., 2018; Lancaster et al., 2015), our results suggest that invasion success is not driven by species' capacity to expand their niche, but rather to conserve it (Bates et al., 2020; Liu, Wolter, Xian, & Jeschke, 2020; Petitpierre et al., 2012). Similar to our results, a recent study on ants (Bates et al., 2020) showed that the propensity to shift the niche is not typically related to the species' ability to cause impacts or spread more broadly. Accordingly, species spread more successfully under environmental conditions they have encountered in their native range (Sychrová et al., 2022), after being released from their competitors.

Overall, our results allow us to pinpoint the main processes shaping the dynamics of niche shifts in invasive species. Despite the long history of plant invasions in Mediterranean Europe, many invasive species have not yet filled the environmental conditions analogous to their native niche. Indeed, the residence time of alien species has little effect on their niche shift dynamics, suggesting that we need to reconsider the effect of residence time and refocus our attention on other aspects of invasions. Specifically, we identified biotic interactions and local adaptations as the main processes influencing niche dynamics during invasions. In addition, we found that the ability of the species to conserve their niche and to establish in the environmental conditions to which they are already pre-adapted (niche filling) is what favours their invasion success most.

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