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Research article

Plant invasion in Mediterranean Europe: current hotspots and future scenarios

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The Mediterranean Basin has historically been subject to alien plant invasions that threaten its unique biodiversity. This seasonally dry and densely populated region is undergoing severe climatic and socioeconomic changes, and it is unclear whether these changes will worsen or mitigate plant invasions. Predictions are often biased, as species may not be in equilibrium in the invaded environment, depending on their invasion stage and ecological characteristics. To address future predictions uncertainty, we identified invasion hotspots across multiple biased modelling scenarios and ecological characteristics of successful invaders. We selected 92 alien plant species widespread in Mediterranean Europe and compiled data on their distribution in the Mediterranean and worldwide. We combined these data with environmental and propagule pressure variables to model global and regional species niches, and map their current and future habitat suitability. We identified invasion hotspots, examined their potential future shifts, and compared the results of different modelling strategies. Finally, we generalised our findings by using linear models to determine the traits and biogeographic features of invaders most likely to benefit from global change. Currently, invasion hotspots are found near ports and coastlines throughout Mediterranean Europe. However, many species occupy only a small portion of the environmental conditions to which they are pre-adapted, suggesting that their invasion is still an ongoing process. Future conditions will lead to declines in many currently widespread aliens, which will tend to move to higher elevations and latitudes. Our trait models indicate that future climates will generally favour species with conservative ecological strategies that can cope with reduced water availability, such as those with short stature and low specific leaf area. Taken together, our results suggest that in future environments, these conservative aliens will move farther from the introduction areas and upslope, threatening mountain ecosystems that have been spared from invasions so far.

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Introduction

The Mediterranean Basin is one of the world's biodiversity hotspots (Mittermeier et al. 2011), but it has been experiencing alien species introduction since historical times (Underwood et al. 2009). This region will also suffer dramatic effects of climate change, with unknown consequences for alien species invasions (Bellard et al. 2018). Invasive plants pose a significant threat to biodiversity by modifying ecosystem functions and structures in ways that are difficult to reverse (Pyšek et al. 2020). These threats have caused an estimated monetary impact in the Mediterranean Basin of approximately USD 10 billion since 1990 (Kourantidou et al. 2021), and both alien species introductions (Seebens et al. 2018) and their impacts are on the rise (Kourantidou et al. 2021). Once established, alien plants are tough to eradicate, which makes prevention measures the most cost-effective form of management (Pyšek et al. 2020). Indeed, tracking the current distributions of the most problematic alien species and anticipating how they might shift in the future (Urban 2020), allows for identifying areas suitable for many potentially invasive species (invasion hotspots) and regions of lower concern (invasion coldspots). Ultimately, this knowledge helps prioritise possible interventions.

Climate change has been shown to be an important driver of the range expansion of alien species (Bellard et al. 2018). The severe climatic changes predicted in Mediterranean Europe, including increasing temperature and decreasing precipitation (Ozturk et al. 2015), could favour alien species over natives since many alien species already present in this region originate from warmer biomes (Cao Pinna et al. 2021) and are typically generalist species with broad climatic tolerances (Gallien et al. 2012, Axmanová et al. 2021). On the other hand, harsh future climates could be just as unfavourable for some alien plants as they are predicted to be for native species (Newbold et al. 2020), leading to changes in both alien species pool and distribution of individual species within focal region (e.g. poleward shifts, Bellard et al. 2018). At the same time, socioeconomic changes such as increasing human population density and propagule pressure could support spread of alien species further away from propagule sources (e.g. cities, coasts), despite less suitable climate conditions. This could result in increased invasion towards inland and mountain areas (Pauchard et al. 2009, Carboni et al. 2018), which have been typically less affected by invasion to date (Petitpierre et al. 2016), and where restraining measures can still be effective.

Not all alien plant species will be equally favoured in future environments. Specific functional traits (van Kleunen et al. 2010) or biogeographic origins (Cao Pinna et al. 2021) may give an advantage to certain species while hindering others. Grouping species with similar traits/geographic origins (Treurnicht et al. 2020) could provide a screening method for identifying successful invaders in Mediterranean Europe based on their ecological characteristics, to identify potential successful invaders not yet included in our list. Typically, invasive plants tend to have competitive traits for rapid resource acquisition, such as large, fast-growing leaves and tall stature, as well as small seeds suitable for long-distance dispersal (van Kleunen et al. 2010, Divíšek et al. 2018). However, hotter and drier future Mediterranean conditions may select for different traits, such as those related to conservative resource acquisition (Axmanová et al. 2021). When traits linked to invasion success are difficult to determine, species phylogenetic position may be an alternative indicator of invasiveness, since many traits and adaptations are shared by related species and within families (such as resistance to disturbances; Guarino et al. 2021, Kalusová et al. 2021, Večeřa et al. 2021). Finally, the biogeographic origin of species could be a proxy of the climatic pre-adaptations of different source pools of species (Arianoutsou et al. 2013, Cao Pinna et al. 2021). Species introduced from the Mediterranean biome might thus have the greatest suitability in current environmental conditions (Feng et al. 2016), while species from hotter or drier biomes could be favoured under future climatic conditions. However, whether alien species' niches are well captured by traits or biogeographic origins in this area has been poorly investigated. Consequently, comprehensive knowledge of the ecological characteristics of successful invaders in Mediterranean Europe is still lacking, limiting the ability of conservation managers to effectively direct efforts on the most dangerous aliens.

Species distribution models (SDMs) capture the relationship between species and their environment to define their ecological niche, which can be used to explore expected invasion scenarios across many species. However, SDMs assume that the modelled species is at equilibrium with its environment, which makes them subject to some biases when applied to alien species that are spreading into a new region. Biased SDM predictions can misdirect management planning, either by prioritizing areas that are not the most threatened (hereafter called geographical bias) or by focusing on less successful alien species (hereafter called taxonomic bias). If alien species have not yet reached all locations suitable for their survival and reproduction (Giulio et al. 2022), compiling distribution data from their global range (global niche) can help reduce biased and underestimated predictions (Gallien et al. 2012, Liu et al. 2020). Yet, this approach might overpredict presences if the invasion is still an ongoing process that is primarily led by spread from specific, locally introduced populations. In this case, modelling the regional niche (i.e. Mediterranean Europe) focusing only on the newly invaded area may be highly relevant to limit current and future overpredictions (Liu et al. 2020, Giulio et al. 2022). By separately estimating both the broader global niche (i.e. using all globally available species occurrence data) and the narrower regional niche included in it, we can assess whether invasion is still ongoing and how modelling choices influence geographical and taxonomic biases. While there has been increased attention given to the issue of model transferability from native to invaded ranges (Broennimann et al. 2012, Liu et al. 2020, Pili et al. 2020), no study has examined whether the biases resulting from projecting models in a new range are mainly geographical or can also cause biases in the ranking of invasive species threat potential (i.e. taxonomic bias).

Here, we estimated current and future scenarios of alien plant invasion in Mediterranean Europe based on predictions of the global and regional niches of the naturalised alien species. Rather than focusing on a single best estimate of invasion risks, we aim to evaluate a conservative scenario (i.e. regional niche) and an extreme scenario (i.e. global niche) to assess which invasions are potentially still ongoing and whether modelling choices lead only to geographical biases or also affect the identification of successful alien species. Then, we aim to answer three questions regarding the current risks and future trends of plant invasions in Mediterranean Europe:

1) Where are invasion hotspots, and how will they shift in the future?
2) Do aliens from different functional groups and with different biogeographic origins have different environmental niches?
3) What are the ecological characteristics of a successful invader under current and future environmental conditions?

Material and methods

Study area and alien species records

The study area includes the Mediterranean biogeographic region in Europe and Turkey as defined by the European Environment Agency (EEA; Cao Pinna et al. 2021). We searched for the occurrence of alien species in 325 000 vegetation plots extracted from the European Vegetation Archive (EVA; Chytrý et al. 2016). We focused on neophytes (species introduced after 1500) with native ranges outside the Mediterranean Basin, identifying 298 alien species. The field-based records in the EVA dataset provide reasonable estimates of the distribution of the most widespread alien species in the region (Axmanová et al. 2021, Cao Pinna et al. 2021). We excluded records older than 1950 and those with location uncertainty > 5 km to match the temporal and spatial scale of the environmental variables. After resampling EVA presences at 30 arcsec (ca 1 km), we removed species with fewer than 30 presences (similar to Gallien et al. 2012). This left us with 92 alien species (Supporting information), for which we extracted global occurrences from the Global Biodiversity Information Facility (GBIF; data accessed in 2020). For GBIF data, we followed the same resampling and filtering procedure as used for the EVA data. Moreover, we further post-processed GBIF data (R package 'CoordinateCleaner'; Zizka et al. 2019) to remove occurrences 1) with clearly erroneous coordinates (e.g. in the sea or with equal longitude and latitude coordinates) or 2) within 1 km from biodiversity institutions (botanical gardens, herbaria, universities, and museums), country centroids and GBIF headquarters. Note that four out of our 92 alien species were also on the list of alien species of Union concern (Supporting information, European Commission Joint Research Centre 2017). The limited number of shared species can be attributed to the different selection protocol we used, which was more focused on data than on impact. However, there is very high congruence between the EU Baseline spatial distribution of invasive alien species of Union concern and the EVA + GBIF presences we obtained for these four species (Supporting information).

Environmental variables

We selected seven variables with limited pairwise correlations (Pearson $R < 0.7$) that capture the limiting conditions of the Mediterranean Basin (Deitch et al. 2017). We chose macroclimatic layers of temperature annual range (bio7), mean temperature of the warmest quarter (bio10), precipitation of the wettest quarter (bio16), and precipitation of the driest quarter (bio17), which we obtained from the CHELSA database at approximately 1 km resolution (Karger et al. 2017). We also acquired the topographic wetness index from the ENVIREM database (1 km resolution, Title and Bemmels 2018) and a layer of soil bulk density from the SoilGrids database (250 m resolution; Hengl et al. 2017). These predictors jointly describe the soil water-holding capacity, an essential variable in arid environments. Finally, we considered population density obtained from the SEDAC database (Jones and O'Neill 2016, at 1 km resolution), which was preferred over other predictors due to its availability for future scenarios. Specifically, to define future scenarios of alien plant invasions, we used future projections for all environmental variables in the year 2050 except for the topographic wetness index and for soil bulk density, which we assumed to remain static in the future at our spatial resolution. To account for differences across future climate scenarios, we used two independent global circulation models (Sanderson et al. 2015), one optimised for the Mediterranean region developed by the Centro Euro-Mediterraneo for Climate Change (CMCC) and another more general for comparability (the Community Earth System Model ver. 1, CESM1), and two possible representative concentration pathways (RCP): the intermediate business-as-usual emission scenario (RCP 4.5) and the worst-case emission scenario (RCP 8.5). These climatic layers were matched with future scenarios of human population density based on corresponding shared socioeconomic pathways (SSP4, an intermediate scenario, and SSP5, the worst-case scenario). The SSPs are complementary narratives of the emissions scenarios and are focused on socioeconomic change (Meinshausen et al. 2020). All variables and species' presences were resampled at a 1 km spatial resolution to avoid mismatch between datasets and, to some extent, mitigate potential sampling biases.

Modelling framework

We used SDMs to estimate the regional niche in Mediterranean Europe and the global niche (which includes all ranges where the species is present: the study region, other invaded areas in the world, and the native range) for each of the 92 alien species. First, to capture the regional niche of each species, we calibrated SDMs combining presences from EVA and GBIF with background data in Mediterranean Europe. Similarly, to capture the global niche as the full suite of environmental conditions to which alien species are potentially adapted, we calibrated global SDMs on EVA and GBIF presences and background data globally (homogenising data sources following Fletcher et al. 2019; see the Supporting information for the relative proportion of points from the two datasets). This global niche is closer to the fundamental niche than the regional niche and has the advantage of capturing all the environmental conditions already globally occupied by the species. Thus, it reduced the risk of underestimating the invasion extent. Comparing predictions based on the global versus the regional niche of species allowed us to 1) provide a consensus map with a higher confidence than the maps solely based on one of these two niches, 2) assess uncertainty across modelling choices, and 3) identify species for which the global model predicts a much larger distribution than the regional one, suggesting the potential for further spread if sustained by new introductions (comparable to high 'unfilling' according to e.g. Petitpierre et al. 2012, but based on the global niche rather than just on the subset of presences in the native range). To complement presences for SDM fitting, we generated two sets of background data: one for the regional niche and one for the global niche. We did not use real absences available in EVA because these were not available globally, and because absences recorded within fine-scale vegetation plots could not be applied in our 1 km modelling resolution (Phillips et al. 2009). Two sets of background points were thus allocated in a buffer area of 100 km around any of the presences (i.e. one buffer for the regional and one for the global dataset) to avoid sampling areas in which alien species were not inventoried (Gallien et al. 2012) and to focus on potentially reachable areas (see the Supporting information for a sensitivity analysis on the buffer dimension, showing limited differences). To further correct different biases in sampling intensities and strategies in the EVA and GBIF databases, we also downweighted background points in poorly sampled areas as described by Phillips et al. (2009; Supporting information). Additionally, we complemented this technique that targeted background data only, with a method that manipulates background and presence data, suggested by Kramer-Schadt et al. (2013) to further mitigate sampling bias. Specifically, we resampled the presences at a resolution of 2.5 arcmin, roughly equivalent to 5 km. We demonstrated that, in our case, these approaches yielded statistically comparable results, predicting similar invaded areas (see the Supporting information for a correlation analysis of the predicted invaded areas using these different methodologies).

To model the potential distribution of each species, we used the R package 'Biomod 2' (Thuiller et al. 2009), which allowed us to examine and aggregate several models jointly. Specifically, for each species, we fitted 18 models for each estimated niche (regional and global) with different setting combinations: 1) three repetitions of 10 000 random selections of background data (but giving equal weight to the presences and the absences); 2) two regression algorithms, GLM and GAM, that have been shown to limit overfit and to be more reliable for future predictions (Brun et al. 2020); and 3) three random split sampling repetitions in which the model was calibrated with 70% of the total data and evaluated with the remaining 30% (several cross-block validation techniques were also tested for comparison, see the Supporting information). The evaluation was performed by measuring the area under the receiver operating characteristic (ROC) curve (AUC, 0–1, where 1 represents systematically right predictions; Swets 1988) and other commonly used evaluation metrics for comparison (both the true skill statistic (TSS), and the Boyce index, showed similar model performance, Supporting information). All 18 models (3 background points generations × 2 regression algorithms × 3 split sampling repetitions $= 3 \times 2 \times 3 = 18$) were projected onto the Mediterranean Basin region and combined to produce one regional and one global niche consensus map for each species. Building consensus projections allowed us to aggregate the intrinsic variability of the modelling process (see the Supporting information for the coefficient of variation within each species predictions as a measure of uncertainty), while also selecting only the best performing models ($AUC > 0.8$). This allowed us to finally create a map of estimated invasion probabilities for each species in Mediterranean Europe (i.e. average probabilities of presences weighted by AUC scores) in current conditions and under future RCP and global circulation models (GCM) scenarios (Thuiller et al. 2009). Moreover, we assessed the potential behaviour of our models in the novel environments with a multivariate environmental similarity surface, and confirmed that the extrapolation in Mediterranean Europe was limited (Elith et al. 2010, Supporting information). Finally, we estimated the importance of each predictor variable by performing three random permutations (Bellard et al. 2016). The modelling workflow is explained in greater detail in the Supporting information following the Zurell et al. (2020) ODMAP protocol.

Future dispersal scenarios

Alien species tend to spread rapidly across the landscape because they often disperse well beyond introduced patches, via their particularly good dispersal abilities, and can cross long distances with human transport (Dainese et al. 2017). Their future distribution driven by climate and socioeconomic changes is expected to fall somewhere between two extreme scenarios: an extreme full-dispersal scenario and a conservative limited-dispersal one. The full-dispersal scenario represents an extreme case where all sites predicted suitable are occupied, and so dispersion limitations are assumed to be negligible (e.g. because of human-aided transportation).

The limited-dispersal scenario represents a conservative case where dispersal limitations are not negligible, with landscape spread mostly driven by species intrinsic dispersal capacities (determined from their traits) and no human-mediated long-distance jumps (e.g. due to a better societal awareness of the invasion threat; Di Musciano et al. 2020). We assessed the natural dispersal distance for each species following Tamme et al. (2014, R package 'dispeRsal'). This method calculates the maximum natural dispersal distance for each species from a linear mixed model with traits as predictors. Specifically, we used dispersal syndrome, life form, seed mass, and plant height as predictive traits (obtained from the TRY database; Kattge et al. 2020). The future distributions for the limited-dispersal scenario were then based on the future suitability maps to those areas predicted as invaded in the current distribution that could be reached by each species, based on their maximum natural dispersal distance, simulating one dispersal event (i.e. just one reproductive event with seed dispersal).

Invasion hotspots and geographical trends

As a measure of invasion risk across Mediterranean Europe, we estimated alien species richness within cells by stacking raw environmental suitabilities of the cell for each species, as suggested by Calabrese et al. (2014), to avoid systematic overpredictions of species richness. Then, to visualise this invasion hotspot map for current and future conditions, we used two arbitrary thresholds of numbers of species (Lyons et al. 2020) to classify coldspots (i.e. < 10 or < 20 species) and hotspots (i.e. > 40 or > 60 species). However, as identifying an arbitrary threshold may create biases, we confirmed the agreement of our maps with maps based on additional thresholds for classifying hotspots (Supporting information, Lyons et al. 2020). We also examined the factors influencing the geography of current and future invasions. To do so, we calculated the correlation (Pearson coefficient) between the environmental suitability of each cell (or its suitability change in future scenarios) and its elevation, as well as its distance from major cities, shorelines, and ports. We measured the distance to each major city included in the Nordpil database (https://nordpil.com/resources/world-database-of-large-cities/), distance to ports based on the Tools4msp database (http://data.tools4msp.eu/), and the distance to the shoreline based on open street maps (https://osmdata.openstreetmap.de). For elevation, we used a digital elevation model (WorldClim database).

Alien niches across functional and biogeographic groups

We tested if species from different functional groups (indicating different ecological strategies) and with different biogeographic origins (indicating different climatic pre-adaptations) have different SDM-predicted niches. For each species, we estimated the probability of occurrence along the range of each environmental predictor separately (projecting the SDM with all variables but one fixed to their mean value; Elith et al. 2005). For each functional group (based on their life form or plant family) and biogeographic origin (Mediterranean/xeric, temperate, and tropical; see details in next section), we averaged species responses to obtain average species niches (and SD confidence intervals) within each group. We then quantified how species responses and confidence intervals to each environmental predictor overlapped within our study area (visually checking the overlap) or differed among functional groups and biogeographic origins (i.e. different source pools).

Identifying the most widespread aliens and their characteristics (present and future)

For each species, we transformed the raw probability distribution in binary maps by selecting the threshold that maximises the AUC (different performance metrics to binarise probabilities gave very similar results, see the Supporting information). Then we calculated the 1) potential range size under current conditions (i.e. number of suitable pixels) and 2) predicted range size change in the future (in percentages compared to the current distribution, i.e. (Gain – Loss)/Current range). We then asked whether functional traits, phylogenetic position, biogeographic origin, or the residence time of each alien species were good predictors of their current environmental suitability and future range size change (Supporting information). As functional traits, we focused on the SLA, plant height, seed mass, life forms (herbs, shrubs, trees), and life cycle (perennial/annual). SLA relates to the ability to exploit resources rapidly (higher SLA values reflect fast growth rates), plant height captures the competitive ability to dominate vegetation by intercepting light, seed mass is related to dispersal distance and establishment success, while life form and life cycle give synthetic estimates of species' ecological strategies (Giulio et al. 2021). For the phylogenetic position, we used the families identified with the R package 'Taxonstand' (Cayuela et al. 2012). To assess species biogeographic origins, we used the biome of origin identified in Cao Pinna et al. (2021) and aggregated species in broader bio-climatic categories (temperate, tropical, and Mediterranean/xeric). Species' residence time was evaluated as the year of the first record in any of the countries of our study area, using the freely available database in Seebens et al. (2017). Then, we fitted a multiple linear model followed by stepwise variable selection based on Akaike's information criterion (AIC) to test the relationship of current potential range size and future range size change with the explored predictors. For the sake of simplicity, we did not include non-linear terms as there was no evidence of non-linearity. Additionally, we provided an overview of the trends (i.e. without performing a variable selection technique) using a dimensionality reduction technique (mixed multiple correspondence analyses, MMCA, R package 'ade4', function *dudi.mix*, Dray and Dufour 2007, www.r-project.org).

Results

Both the regional (AUC mean = 0.92, SD = 0.04, and TSS mean = 0.71, SD = 0.093) and global niche models (AUC mean = 0.96, SD = 0.02, and TSS mean = 0.80, SD = 0.079) had good predictive performances (see the Supporting information for a comparison with other cross-block validation techniques on selected species). The global models showed slightly better performances. As expected, the global models defined the worst scenarios of invasion with wider hotspots completely including those of the regional model (Fig. 1; see the Supporting information for the consensus map among models). The global niches estimated 42% of the study area to be suitable for more than 40 alien species, while this value dropped to 18% in the model with regionally assessed niches. Conversely, based on regional and global niche models, 56 and 3% of the study area, respectively, were predicted to have a low invasion level. However, the models agreed qualitatively in the geographical distribution of the hotspots and coldspots across Mediterranean Europe (Fig. 1, Supporting information). In addition, the models also largely agreed in identifying the same most widespread species (e.g. *Ailanthus altissima*, *Amaranthus albus*, *Bidens aureus* and *Euphorbia prostrata*). Nevertheless, several species had high predicted suitability according to the global niche model but low suitability according to the regional model, suggesting a high potential for further expansion (e.g. *Ambrosia psilostachya*, *Panicum capillare*, *Amorpha fruticosa*, and *Acer negundo* may continue to invade, in decreasing order, from 60 to 38% of Mediterranean Europe). Our results show that estimating different niches can affect predictions mainly quantitatively, resulting in biased geographical projections that do not affect the identification of the most successful invaders (low taxonomic bias).

Models under both intermediate and worst-case emissions scenarios (i.e. RCP 4.5 and RCP 8.5) for 2050 projected a

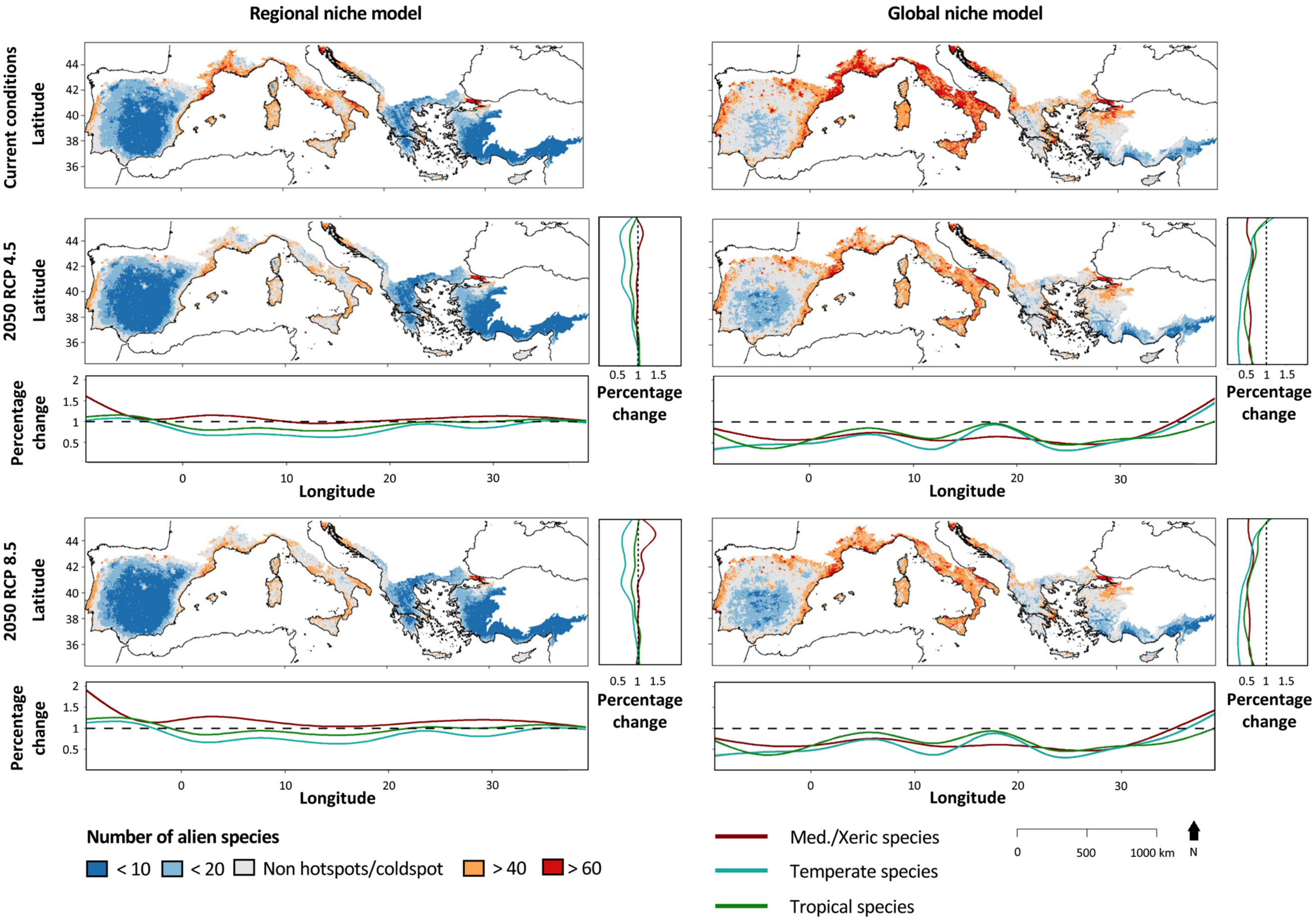

Figure 1. Invasion hotspot maps for the current conditions and future intermediate and worst-case scenarios (i.e. representative concentration pathways (RCP) 4.5 and 8.5) for 92 modelled alien species. To derive a synthetic estimate, we averaged the mean occurrence probability of the two global circulation models (GCM), i.e. Community Earth System Model 1 (CESM) and Centro Euro-Mediterraneo for Climate Change (CMCC) predictions for each species to obtain only two maps, one for each RCP. Finally, we represented latitudinal and longitudinal trends in the range change pattern to test for species' geographic movements (e.g. poleward shifts) in our study area that is northward clipped at the limits of the Mediterranean biogeographical region. Specifically, we calculated the mean of species' richness percentage change in cells predicted to remain invaded under future scenarios (i.e. for a value of 2, the number of species will, on average, double). These range change values were aggregated for species' biomes of origin (i.e. 13 Mediterranean, 49 temperate and 30 tropical species) and displayed in the side insets of the maps.

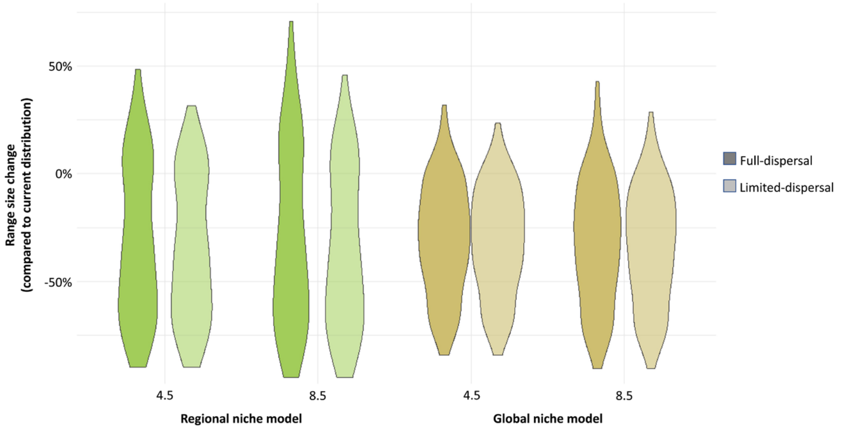

Figure 2. Violin chart showing the expected range size change (in percentages compared to the current distributions, i.e. (Gain – Loss)/Current range) in the different explored scenarios (i.e. for the regional and global niche models). Positive values of the range size change indicate a predicted increase in the suitable area of invasions, while negative values indicate a decrease. The graph shows the intermediate (representative concentration pathway (RCP) 4.5) and the worst-case (RCP 8.5) emission scenarios and the full-dispersal and limited-dispersal predictions.

comparable decrease in invasion (Fig. 2). We found that the full-dispersal and limited-dispersal scenarios (in which future projections were constrained by species dispersal distances, Fig. 2) and the two GCMs (Supporting information) strongly agreed on predictions. Invasion hotspot areas were predicted to decrease by almost 10%, while the coldspots were predicted to increase by 4 to 13 % depending on the niche and emission scenario (Fig. 1). Yet, both models predicted that some alien species would greatly enlarge their suitable area, compared to their current distribution (e.g. *Acacia saligna* by 36%, *Ageratina adenophora* by 34%, *Digitaria ciliaris* by 32%, *Amaranthus viridis* by 21%). Given the qualitative similarity between model predictions, in the following, we will present results from the global niche model (worst-case scenario) and for the full-dispersal intermediate emission scenario of future trends (averaged across GCMs).

Where are invasion hotspots, and how will they shift in the future?

Overall, the invasion hotspot maps show that Mediterranean Europe currently has high environmental suitability for the selected alien species. Mediterranean Italy, France, and the central Mediterranean islands, as well as north-western Turkey and the eastern coast of Spain, are invasion hotspots (Fig. 1). Coldspots are mainly located in central Spain and the southern, mountainous parts of Turkey and Greece. Moreover, we found that invasion hotspot distribution was negatively correlated (Pearson's R= −0.4) with distances to ports and the coast (these two predictors were highly correlated: R = 0.98), indicating that current coastal areas are highly suitable for alien species. Similarly, most invasions were predicted to occur at low elevation (R = −0.3). Considering future projections, suitability for the modelled species will increase at higher elevations (R = 0.56), while decreasing sharply at cities, and at ports at sea level or the coast (R = 0.05 for all). This increase in the number of established alien species will occur mainly above 1500 m a.s.l. for all Mediterranean Europe, with a geographically uniform upward shift of the hotspots (Fig. 3a–b).

Do aliens from different functional groups and with different biogeographic origins have different environmental niches?

Response curves (i.e. SDM-predicted niches) revealed coherent responses of species within broad biogeographic groups (i.e. with similar climatic pre-adaptations) and different responses between these groups (number of species in each group: Mediterranean = 13, temperate = 49, tropical = 30). Specifically, Mediterranean/xeric and tropical species had similar niches, surviving best where seasonal variation was small, the temperatures in the warmest quarter were high, and the areas were arid (particularly in the case of Mediterranean/xeric species; Fig. 4). In contrast, temperate species preferred pronounced seasonality and were less tolerant of warm and arid conditions (Fig. 4). All alien species responded positively to propagule pressure. However, the relative importance of each predictor showed that the relationship with propagule pressure was weaker for Mediterranean/xeric species (Fig. 4b), and the distribution of temperate species was strictly limited by precipitation in the driest quarter and less constrained by seasonality. In contrast, species from the tested functional groups and families did not differ as markedly in their responses to environmental gradients (Supporting information).

What are the ecological characteristics of a successful invader under current and future environmental conditions?

None of the species' traits we studied (SLA, plant height, seed mass, life form, and life cycle) nor species biogeographic origin were good predictors of the current modelled range size in our best model ($F_{3,89} = 2.9$; $p = 0.04$; $R^2 = 0.09$, Fig. 5a). In

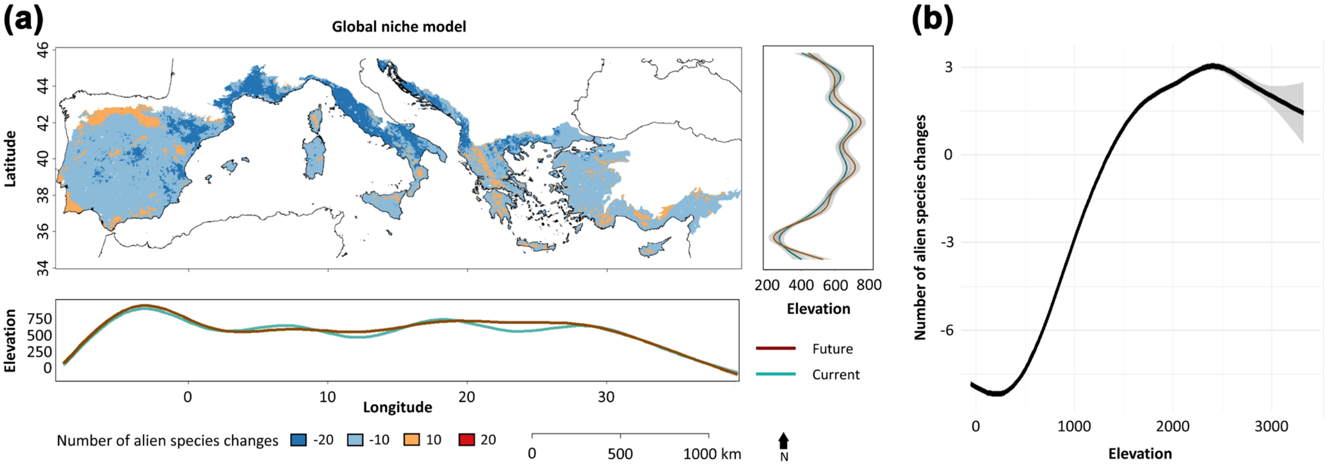

Figure 3. (a) Net changes in the number of currently established alien species from current to future invasion, for the global niche model and intermediate emission scenario (red values indicate an increase in invasion, and blue values indicate a decrease). The side plots show the third quantile of the elevation of the areas with more than 40 species (i.e. hotspots) for current (light blue) and future (brown) conditions. (b) Results of a generalized additive model (GAM) model showing changes in the number of invaders at each elevation. Results are evaluated by comparing the current and future intermediate emission scenarios for the global niche model.

contrast, the phylogenetic position allowed us to differentiate between successful and less widespread invaders. In particular, alien species from the Amaranthaceae family (n = 9) showed higher environmental suitability (Fig. 5a). Nevertheless, and complementary to our analyses, the mixed multiple correspondence analyses also revealed a trend toward higher environmental suitability for shrubs and Mediterranean/xeric alien species (see the Supporting information for results and methodological details).

In contrast, the best model for future change in species range size included species height and seed mass, life form, family, and biome of origin as good predictors ($F_{9,82} = 3$; $p < 0.001$, $R^2 = 0.25$; Fig. 5b). The model showed that woody species, Poaceae, shorter, and Mediterranean/xeric species would be less negatively impacted or even favoured by future environmental conditions. Specifically, Mediterranean/xeric species will likely have a peak of expansion at longitudes above 42°N and a slight increase in western Spain, unlike temperate and tropical species, which will tend to homogeneously decrease across longitude and latitude (Fig. 1, a trend mainly captured by the regional niche model). Moreover, the mixed multiple correspondence analyses (explained variability of the first two axes: 34%; Supporting information) confirmed the linear model's trend and revealed that the most disadvantaged alien species under future conditions also tend to have high SLA.

Discussion

Our study provides the first estimation of the environmental suitability of Mediterranean Europe for the alien plant species currently present in the area. Most of the currently well-established aliens will be affected by future climatic and socioeconomic changes. However, alien species that can tolerate reduced water availability will spread significantly. In addition, many alien species will move northward and upslope in response to climate change, spreading away from propagule sources and threatening fragile mountain ecosystems. Finally, our results show that the different biases of the global and regional niche models result in quantitatively different geographic projections that potentially can jeopardise management efforts but not the identification of the most widespread species.

Overall, species distributions based on regional niche models were a subset of the distributions based on the global niche of alien species (i.e. the worst-case scenario). However, the two sets of models predicted the same successful invaders (currently most widespread) and climate change-favoured species, thereby highlighting species that have high current suitability (e.g. *A. altissima, A. albus, B. aureus, E. prostrata*) and those that have a high potential to spread in the future (e.g. *A. saligna, A. adenophora, A. viridis, D. ciliaris*). The potential spread of the latter group can still be stopped by management actions. Thus, our results suggest that biases related to using the broader global or the narrower regional niche model would not impair the correct identification of the most invasive species, which is encouraging for compiling lists of alien species of pan-Mediterranean interest, but also for global applications (Pyšek et al. 2020). Nevertheless, results of regional versus global models also show differences in the size of the suitable area for many species, which are important for indicating invasion risk (Gallien et al. 2012, Petitpierre et al. 2012). Similarly to what Sychrová et al. (2022) found for North American trees introduced to Europe, many of the alien plants we studied have the potential for further spreading, as they currently occupy only a small portion of the environmental conditions to which they are globally adapted (i.e. incomplete invasion, partially comparable to high 'unfilling' of the native niche according to Petitpierre et al. 2012).

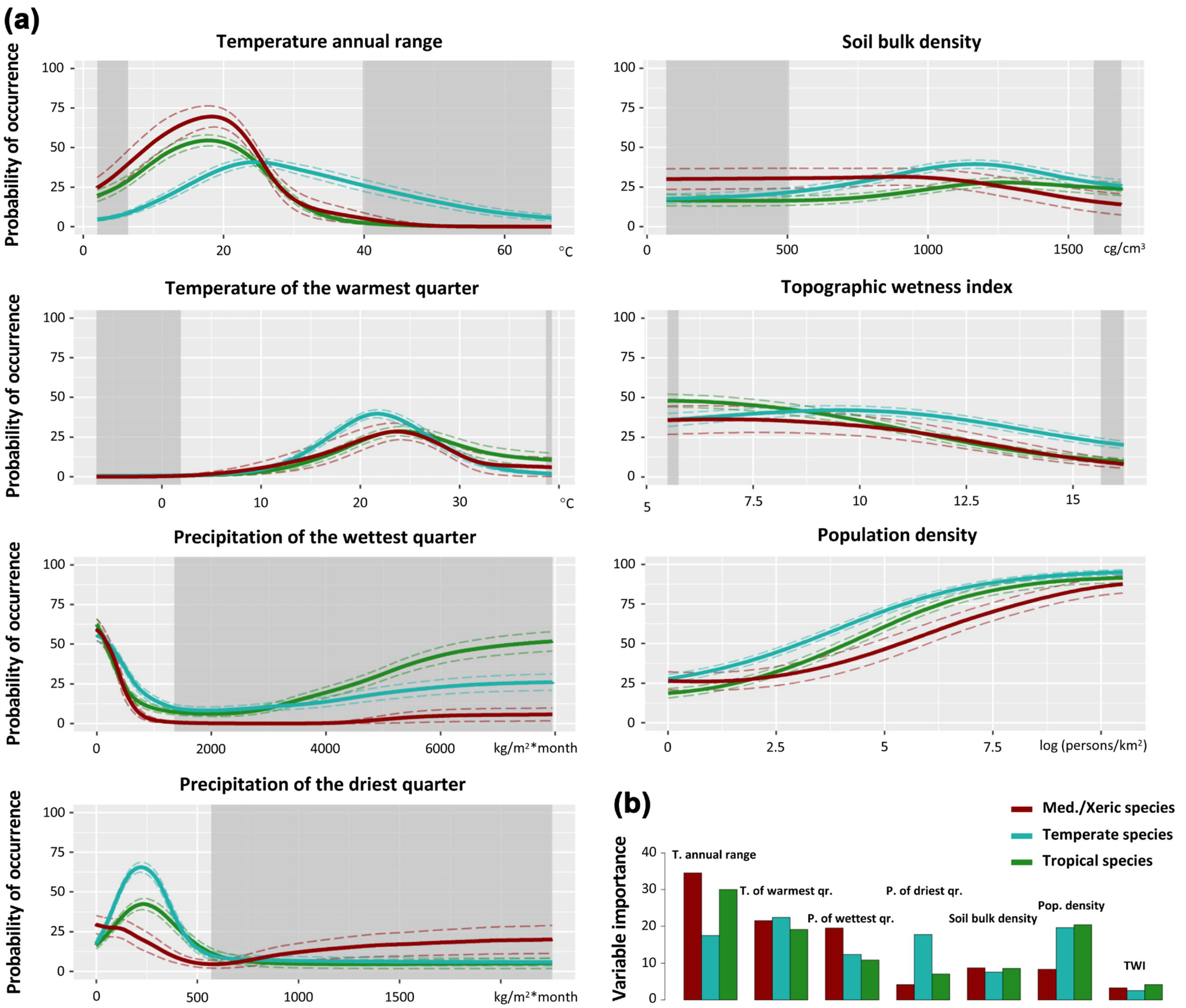

Figure 4. (a) Response curves aggregated for species' biomes of origin (13 Mediterranean, 49 temperate and 30 tropical species), showing the relationship between each variable and the mean of the probability of occurrence (i.e. environmental suitability) with the estimated confidence interval (dashed line). Specifically, we projected the species distribution model (SDM) with all variables but one fixed to their mean value (Elith et al. 2005). The dark grey shaded areas in the background indicate environmental space outside the range of environmental conditions currently present in Mediterranean Europe. (b) Mean values of variable importance aggregated for species' biomes of origin. Results are based on the global niche model.

The global study by Petitpierre et al. (2012) found that most terrestrial plant species largely conserved their niche during invasion. However, they also reported that almost half of the species still left a high proportion of their native niche unfilled in the invaded range. This high unfilling may represent an 'invasion debt' which will eventually be paid with time (Essl et al. 2011, Giulio et al. 2022), for example if these species are sustained by new introductions from different regions of the world or develop local adaptations. For example, for *A. psilostachya*, our regional model predicts a smaller distribution than the global model, with a potential (i.e. if the species will be able to fill its global niche) for further expansion in 60% of Mediterranean Europe. The species is currently only sporadically found in Mediterranean Europe, but it is likely overlooked by botanists (Gerber et al. 2011). These results suggest that management strategies should consider a range of possible invasion scenarios based on different modelling choices (Malavasi 2020, Muscatello et al. 2021). As our global model represents the worst-case scenario, a precautionary approach would be to base conservation actions on the broader predictions of the global model.

Consistent with previous research, we found a high potential for widespread invasions in lowland regions near coasts and ports (Dawson et al. 2017, Schneider et al. 2021). In these regions, the environmental suitability combined with the high propagule pressure has resulted in the introduction

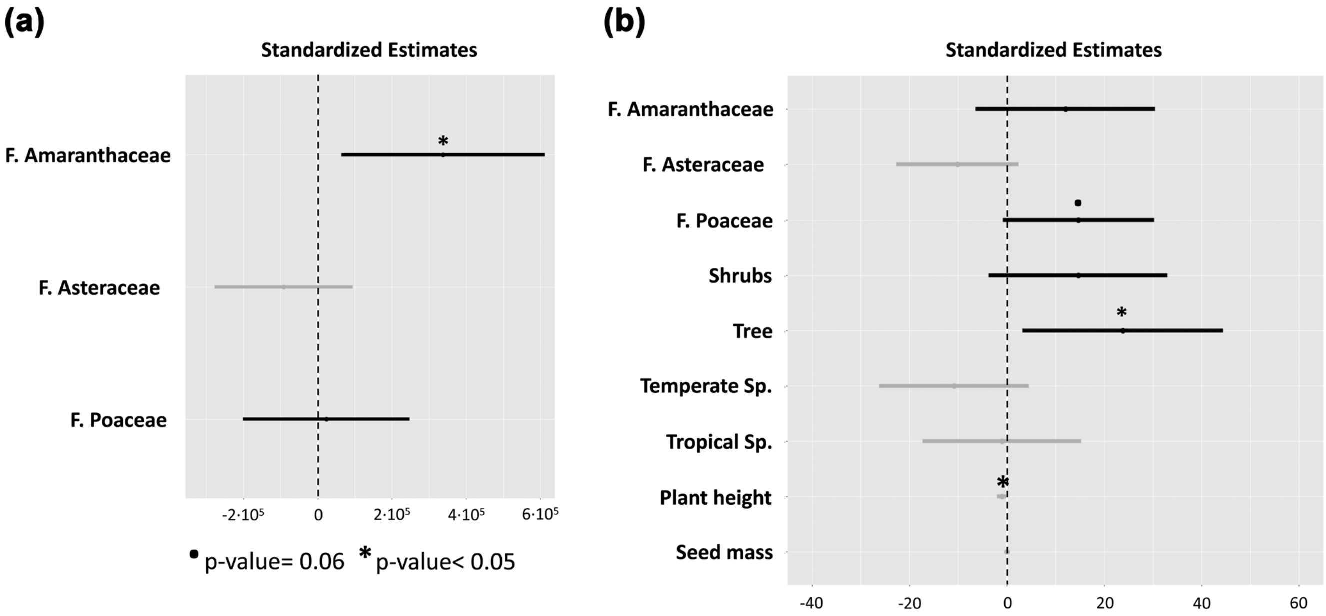

Figure 5. Standardised estimates (± SE) for each predictor of the multiple linear regression for (a) current and (b) future range size change. Estimated values for the categorical variables are compared to herbs for the life forms (number of species: herbs = 72, shrubs = 8, trees = 12), to Mediterranean/xeric species for the biomes of origin (number of species: Mediterranean = 13, temperate = 49, tropical = 30), and to other families combined for the family (number of species: Amarathaceae = 9, Asteraceae = 26, Poaceae = 15, Other = 42). Black and grey bars represent positive and negative relationships, respectively.

and spread of many invasive species (Pyšek et al. 2020). In terms of future projections, our results are in line with many large-scale studies that predict a decrease in environmental suitability for most already established alien plants with a potential for fewer aliens to significantly expand (Bellard et al. 2018, Lopez et al. 2022). However, many currently established alien species will move northwards (Urban 2020) and to higher elevations (Petitpierre et al. 2016, Carboni et al. 2018), driven by changing climate. The predicted upslope shifts are in line with several field studies (Pauchard et al. 2009) that have shown this process to already occur in many mountain ranges worldwide, including the Swiss and French Alps (Petitpierre et al. 2016, Carboni et al. 2018). Here, we show for the first time at a broad geographic scale that this trend will likely further increase across the Mediterranean region of Europe. Given that alien species could impose a new threat to vulnerable mountain ecosystems, which have not been highly invaded so far, future management actions should be focused on restraining propagule pressure and mitigating alien species invasion in Mediterranean mountainous areas (Carboni et al. 2018).

It is important to note that our results indicating a future reduced environmental suitability for the modelled alien species may be somewhat biased because of two methodological issues. First, we only focused on alien species currently widespread in Mediterranean Europe, but it is possible that newly emerging invaders or less common aliens already established in the study area will take advantage of the novel environmental conditions (Seebens et al. 2018). For example, among the species we had to exclude because they are currently rare, a few had traits that suggest they could spread in the future (three were phanerophytes from other Mediterranean biomes, and ten were short annual grasses). In this context, our results on the characteristics of the successful invaders could be helpful for screening the potentially most dangerous species ahead of time. Additionally, some well-adapted, non-generalist aliens in under-sampled eastern Turkey could be excluded by our species selection criteria that focused on relatively frequent species. This likely results in only a small and spatially constrained underestimate of the current degree of invasion in some areas, such as eastern Turkey, but may have unknown implications for future predictions (although the global model seems to be more robust to geographic biases; Supporting information). However, we assume that the species selection has only limited confounding effects on our results, as other studies using different selection criteria have found similar patterns (Dawson et al. 2017, Bellard et al. 2018, Lososová et al. 2018, Pouteau et al. 2021, Schneider et al. 2021, Wagner et al. 2021). Similarly, new invaders and less common alien species are likely still in a time-lag phase and will need time to naturalise, having marginal effects on our 2050 projections even if environmental and socioeconomic filters changed (Haeuser et al. 2018, Wallingford et al. 2020). A future improvement in this regard could be to develop future predictions of a more comprehensive human footprint variable (Weiss et al. 2018), which would replace the human population density by a measure more tightly related to propagule pressure. Second, SDMs generally do not capture the response of alien species to novel climates and non-analogous climate combinations (Pouteau et al. 2021), which likely leads to an underestimation of the effects of phenotypic plasticity, changes in biotic interactions, and evolutionary adaptation in predicting future species distributions (Des Roches et al. 2018, Garzón et al. 2019). Here we attempted to overcome this limitation by estimating the global niche of species, thereby capturing all known species responses to climate combinations.

Based on the environmental response curves, we found that Mediterranean/xeric and tropical species featured different ecological strategies than temperate species. The former two groups had high suitability, whereas temperate species were disadvantaged (Guarino et al. 2021), preferring a marked seasonality and being less tolerant to warm and arid periods (Fig. 4a). We also found that human density was a less important predictor for Mediterranean/xeric species, probably because these species occur globally in both human-disturbed and natural environments (Guarino et al. 2021). Indeed, pre-adaptation to human-disturbed environments at the global scale is an important predictor of naturalisation and the invasion potential of alien species (Kalusová et al. 2021). In contrast, although many studies identified a relationship between species niches and their traits (van Kleunen et al. 2010, Treurnicht et al. 2020), we found no differences in niches of alien species in the Mediterranean region based on a broad range of functional traits. It is possible that neither the individual generic traits selected (e.g. life forms) nor the phylogeny were sufficient to fully capture species niches without considering trait combinations or interactions (e.g. interactions among traits or habitat-specific responses; Funk et al. 2016).

Nevertheless, specific functional traits (e.g. SLA and plant height) and phylogeny combined with biogeographic origins allowed us to predict the suitable habitats for alien plants under current and future conditions in Mediterranean Europe. Our results are consistent with other global-scale analyses showing that alien species typically share the same adaptations as native species. In our case, this adaptation was the ability to conserve water, which favoured Mediterranean/xeric evergreen shrubs with sclerophyllous leaves. Along with climatic pre-adaptation, adaptations to cope with human-disturbed environments (Kalusová et al. 2021) are key to a successful invasion in Mediterranean Europe. Indeed, the advantage of Amaranthaceae (only represented by the genus *Amaranthus* in our data) in human overexploited areas may be related to their C4 metabolism (Sage et al. 2007), resistance to drought, abundance in soil seed banks, and introduction as crop weeds (Assad et al. 2017, Kalusová et al. 2021). Shrub and tree alien species could benefit from current and future Mediterranean climates, probably because of their broad ecological niche and ability to conserve resources, high introduction pressure over time, and relation with human management practices (Guarino et al. 2021, Wagner et al. 2021). Nevertheless, we found that most alien species are annual or perennial herbs (Arianoutsou et al. 2013, Funk et al. 2016), which could better establish in habitats with strong biotic constraints and with fine-scale temporal changes in resource availability (Feng et al. 2016, Galán Díaz et al. 2021). Our results suggest that taller and more acquisitive plants with high SLA are not widespread and will be disadvantaged in future climates (Carboni et al. 2018). In fact, in drought-prone Mediterranean environments, photosynthesis could be more strongly limited by water than light, and belowground traits (e.g. root length and distribution) may be better candidates to characterise successful invaders (Funk et al. 2016), although data on these traits are often not available for many species. Finally, we found that species from the family of Poaceae – as this family is supposed to have originated in tropical regions – would benefit from future warmer environments (Bouchenak-Khelladi et al. 2010, Večeřa et al. 2021). They are resilient species with broad climatic tolerances; resistant to fire, drought, and frost; are adapted to both cold and hot, dry environments depending on their photosynthetic modes (C3 versus C4); and have a competitive root system (Linder et al. 2018).

In conclusion, the current invasion hotspots, mainly found in the central regions of the Mediterranean Basin, as well as on the coast of Portugal and the Bosphorus area, will likely change in future due to projected environmental changes. Plant invasions will become an issue in areas where they were historically not considered a threat, particularly in the mountains. These changes will potentially be accompanied by the spread of currently established species in the environmental conditions to which they are globally adapted or by novel species introductions. New species that are likely to become problematic and widespread if introduced in the future are mainly those with conservative use of resources, such as short grasses or trees with low SLA. Finally, our approach shows that modelling biases do not affect the correct prioritization of the worst alien species, which is encouraging for preparing future lists of alien species. Overall, these results pave the way for identifying successful invasion control strategies in a biodiversity hotspot subject to multiple global change pressures. More broadly, our approach – combining SDMs for currently widespread alien species with scenario modelling and the analysis of species traits and biogeography – offers a framework to overcome the limitations and biases of future invasion predictions.

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Luigi Cao Pinna: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Validation (lead); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Laure Gallien**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting);

Writing – review and editing (supporting). **Laura J. Pollock**: Conceptualization (supporting); Investigation (supporting); Writing – original draft (supporting). **Irena Axmanová**: Data curation (supporting); Investigation (supporting); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Milan Chytrý**: Resources (equal); Supervision (supporting); Visualization (supporting); Writing – original draft (supporting). **Marco Malavasi**: Investigation (supporting); Supervision (supporting); Visualization (supporting). **Alicia T. R. Acosta**: Conceptualization (supporting); Funding acquisition (equal); Project administration (supporting); Resources (supporting); Supervision (supporting). **Juan Antonio Campos**: Resources (supporting); Validation (supporting); Writing – original draft (supporting). **Marta Carboni**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (supporting); Software (supporting); Supervision (lead); Validation (supporting); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

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Data availability statement

Original data include the following environmental and spatial layers: shapefiles of the world's coastlines (https://osmdata.openstreetmap.de), ports (http://data.tools4msp.eu/layers/geonode%3Aport_pt_2013) and cities (https://nordpil.com/resources/world-database-of-large-cities), as well as gridded data of present-day and future climate (https://chelsa-climate.org), topographic wetness index (https://envirem.github.io) and soil bulk density (https://data.isric.org), elevation (www.worldclim.org) and population density (http://sedac.ciesin.columbia.edu/data/set/popdynamics-1-km-downscaled-pop-base-year-projection-ssp-2000-2100-rev01/data-download). Plant occurrence records and vegetation survey data were obtained from GBIF (GBIF.org, 3 October 2020, GBIF Occurrence Download: https://doi.org/10.15468/dl.mdkwsz) and the European Vegetation Archive (EVA). Data from EVA can be obtained by application to the EVA database administrator according to the EVA Data Property and Governance Rules (http://euroveg.org/eva-database-obtaining-data) and specifying the project reference no. 85 (http://euroveg.org/eva-database-eva-projects).

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j0zpc86j1 (Cao Pinna et al. 2024).

Supporting information

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

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