Beyond tracking climate: niche evolution during native range expansion and its implications for novel invasions

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Abstract

Ecological niche models have been instrumental in understanding and forecasting the widespread shifts in species distributions under global change. However, growing evidence of evolution in spreading populations challenges their key assumption of niche conservatism, limiting model transferability in space and time. Climate niche evolution has been studied extensively in invasive species, but may also occur in native populations tracking climate change, when species encounter novel abiotic conditions that vary with latitude. We compared niche shifts during native range expansion and during invasion in *Dittrichia graveolens*, a Mediterranean annual plant species that is currently undergoing both types of spread. We asked whether the species' northward native range expansion in Eurasia matched climate change from 1901-1930 to 1990-2019, or if further range expansion was promoted by niche evolution. In addition, we asked how niche expansion in the native range affected forecasts of two ongoing invasions in Australia and California. We quantified niche shifts in environmental space using the analytical framework of niche centroid shift, overlap, unfilling, and expansion (COUE), and examined associated distribution changes in geographic space using Maximum Entropy modeling. Our results show that *D. graveolens* expanded its native range well beyond what would be sufficient to track

climate change, a shift associated with a 5.5% niche expansion to include more temperate climates. In contrast, both invasions showed evidence of niche conservatism, with niche filling depending on invader residence time. Including the expanded native niche in invasion projections added new areas at risk of invasion, but none of these has been colonized at present. We conclude that native populations may track climate change and adapt to novel local conditions in parallel, causing an evolutionary expansion of the climate niche and more widespread range expansion than expected based on climate change alone.

Keywords

Range shift; climate change; invasion; niche evolution; range expansion; habitat suitability

Introduction

Forecasting the widespread distribution shifts of both native and invasive species under global change represents one of the major challenges in biodiversity conservation (Urban et al. 2016). The climate niche has become a central concept in modeling efforts to understand species' preferred climate conditions, where such suitable habitat will be present under future climates, and which areas are at risk of invasion on other continents (Elith and Leathwick 2009). Ecological niche models (ENMs; also known as habitat suitability models or species distribution models) are widely used and applied to conservation planning (Araújo et al. 2011). However, range-expanding populations have been demonstrated to rapidly adapt to novel environments in a growing body of empirical studies (reviewed in Colautti and Lau 2015, Chuang and Peterson 2016), challenging the fundamental assumption of ENMs that niches are conserved in space and time (Pearman et al. 2008). Newly developed mechanistic and hybrid species distribution models

that incorporate evolution of species' physiological limits (Hoffmann and Sgrò 2011, Catullo et al. 2015) predict markedly different outcomes of climate-induced range shifts (Bush et al. 2016) and invasions (Kearney et al. 2009) than traditional correlative ENMs. While there is thus a compelling argument for incorporating evolution into range expansion forecasts (Nadeau and Urban 2019), a better understanding of the degree to which climate niche evolution promotes contemporary range expansions is necessary to make informed predictions.

Niche evolution has been studied extensively in invasive species, with studies comparing the climate conditions occupied by populations in the native and invaded range. While there is strong evidence that invading populations can rapidly evolve to reestablish adaptive clines along environmental gradients similar to those in their native range (e.g., Boheemen et al. 2019), whether species' ultimate niche limits are generally conserved during invasion (Petitpierre et al. 2012, Liu et al. 2020) or commonly shift (Early and Sax 2014, Atwater et al. 2018) is highly debated. Niche stasis (*sensu* Pearman et al. 2008) is defined as the lack of change in either the fundamental niche (the climate where a species can grow in the absence of biotic constraints and geographic barriers) or realized niche (the actual climate conditions where a species is observed, which is captured by ENMs). Niches may shift in the invaded range when not all areas with similar climates are occupied (yet) due to dispersal limitation. Niche expansion occurs when biotic interactions or dispersal barriers constraining the realized niche in the native range are lifted in the new range, or when the fundamental niche itself evolves (Alexander and Edwards 2010). Examples of evolutionary changes that have been linked to climate niche expansion in invasive populations include plant phenology responses to temperature or photoperiod (Dlugosch

and Parker 2008a, Colautti and Barrett 2013) and insect thermal and moisture tolerance (Kearney et al. 2009, Hill et al. 2013).

Much less attention in the empirical literature has been paid to niche evolution during contemporary native range shifts induced by climate change. Instead, species' responses to global warming are commonly viewed as a "move, adapt, or die" conundrum, where populations need to track suitable climates to higher latitudes and altitudes, or adapt *in situ*, or else they will lag behind the pace of climate change and go extinct (Aitken et al. 2008, Corlett and Westcott 2013). However, poleward-spreading populations face a variety of novel abiotic (as well as biotic) conditions, even if range expansion is initiated by climate change (Spence and Tingley 2020). For example, photoperiod and temperature seasonality increase non-linearly with latitude, and plants experience a reduction in photosynthetically active radiation and light quality towards the poles (Taulavuori et al. 2010, Saikkonen et al. 2012). These novel combinations of temperature and photoperiod cues at higher latitudes require a plastic or evolutionary response (Visser 2008). Thus, whether climate-mediated range shifts will involve simultaneous niche evolution is now acknowledged as an important open question (Lee-Yaw et al. 2019, Nadeau and Urban 2019). Recent empirical work has demonstrated rapid evolutionary responses to novel abiotic conditions during contemporary native range shifts, including increased thermal niche breadth in damselflies (Lancaster et al. 2015, Dudaniec et al. 2018) and earlier fall phenology in plants (Lustenhouwer et al. 2018). Palaeoecological studies of the Pleistocene glaciations have shown that dispersal, plasticity, evolution and niche conservatism have all played a role in past range shifts with climate change (Martínez-Meyer et al. 2004, Nogués-Bravo et al. 2018).

Historic constraints (or the lack of them) on range expansion may inform how evolution will affect recent range shifts with climate change (Diamond 2018).

Comparing native range shifts and invasions provides valuable insights into the drivers of niche evolution during range expansion in both native and exotic ranges. Quantifying rapid adaptation to novel climates during invasions can inform predictions about the degree of evolutionary change that may be expected during native range expansions on similar time scales (Moran and Alexander 2014). Similarly, the likelihood of niche shifts in the invaded range depends on whether the native range is limited by biotic interactions or fundamental evolutionary constraints such as genetic correlations between traits (Alexander and Edwards 2010). Yet there are also differences between native and exotic range expansions in key processes driving evolutionary change, most notably the level of gene flow. Disconnection from the historic native range could lead to increased niche evolution in invading populations (Jakob et al. 2010), unless genetic diversity and population sizes are too low (Hoffmann and Sgrò 2011). However, genetic bottlenecks have little impact in invasions founded by multiple introductions (Dlugosch and Parker 2008b, Smith et al. 2020). In the native range, the impact of ongoing gene flow will depend on whether it has a maladaptive swamping effect or increases evolutionary potential, an issue which is highly debated (Kottler et al. 2021). Theory suggests that adaptation during range expansion under gene flow is governed by the balance between selection and genetic drift on the one hand, and the steepness of the environmental gradient on the other hand (Polechová and Barton 2015). Overall, authors have hypothesized that niche shifts are more common or rapid in exotic than in native range expansions (Pearman et al. 2008, Wiens et al. 2019), but the empirical data required to test this idea are largely absent.

In this study, we examine climate niche evolution during both native and exotic range expansion by taking advantage of a species currently involved in both types of population spread. *Dittrichia graveolens* (L.) Greuter is an annual plant in the Asteraceae with a native distribution around the Mediterranean Basin (Brullo and De Marco 2000). The species has greatly expanded its native range northward since the mid-20th century, coincident with rapid evolution of earlier flowering time at the leading edge in response to shorter growing seasons (Lustenhouwer et al. 2018). *D. graveolens* has a ruderal life history and produces large numbers of wind-dispersed seeds, facilitating spread along roads where biotic interactions with other plant species play a minor role in its ecological success. The species has invaded worldwide in most other regions with a Mediterranean climate - first Australia (1860s; Parsons and Cuthbertson 2001) and South Africa (GBIF.org 2020), then California (1980s; Preston 1997), and most recently Chile (Santilli et al. 2021). In Australia and California, *D. graveolens* is considered a noxious weed of high management concern due to a combination of rapid spread and toxicity to livestock, impacts on native plant communities, and human skin allergies (Parsons and Cuthbertson 2001, Brownsey et al. 2013b, USDA 2013).

We ask: (a) Did *D. graveolens* simply track climate change during the native range expansion, or was range expansion promoted by climate niche evolution? (b) Is there evidence of niche shifts in the invaded ranges? (c) How does taking into account climate niche evolution during the native range expansion change invasion predictions for California and Australia? To answer these questions, we applied the COUE scheme of niche centroid shift, overlap, unfilling and expansion (Guisan et al. 2014) to *D. graveolens*' native range expansion with climate change (comparing the periods 1901-1930 and 1990-2019) and to the two exotic range expansions. This

method quantifies niches in environmental space and is widely used to study niche dynamics of invasive species. In addition, to explore niche shifts during range expansion in geographic space, we fit species distribution models using maximum entropy modeling (Maxent), which was specifically designed for presence-only data (Phillips et al. 2006). Based on prior evidence for rapid evolution of phenology at the northern range edge (Lustenhouwer et al. 2018), we hypothesized that *D. graveolens*' climate niche expanded during native range expansion in Eurasia. We expected greater niche filling and greater niche expansion in Australia than in California, due to *D. graveolens*' much longer invasion history in the former region. Finally, we hypothesized that forecasting the two invaded distributions based on the newly expanded native range would increase our invasion risk assessment for a wider range of climates and geographic areas.

Material and Methods

Data collection

Occurrence data

We compiled presence-only species occurrence data for *Dittrichia graveolens* (L.) Greuter and its nomenclatural synonyms *Inula graveolens* (L.) Desf., *Cupularia graveolens* (L.) Godr. & Gren., and *Erigeron graveolens* (L.). We used the Holarctic Floral Kingdom (Cox 2001) as our study region (split between Eurasia/North Africa for the native range and North America for one of the invaded ranges), to take into account the broadest range of environments available to *D. graveolens* in its evolutionary history and facilitate projection of our models to other continents (Merow et al. 2013). This study region also allows for comparison to other studies using the same spatial extent (Petitpierre et al. 2012). Our primary data source was the Global Biodiversity

Information Facility (~75% of occurrences; GBIF.org 2020), supplemented by country-level species occurrence databases (FloraWeb 2013, Nikolić 2015, Zając and Zając 2019, BSBI 2020, Info Flora 2020), standard floras, articles in botanical journals, and herbarium records. All citizen science records from iNaturalist in GBIF were verified manually (iNaturalist 2020). We used QGIS v3.8.2 (QGIS Development Team 2019) to combine and convert all data to the WGS84 coordinate system with decimal degrees latitude and longitude. Spatial grids (UTM, MTB, etc.) were imported as cell centroids. To increase sampling density across the study region, we also georeferenced localities without spatial coordinates (such as towns and other geographic features described in sufficient detail) using GEOLocate (Rios 2020). Data quality control included the removal of duplicate records and those located at (0,0) degrees or country centroids. The final (expanded) native range dataset included 8157 occurrences. To study niche shifts in the exotic range of *D. graveolens*, we selected the invasions in Australia and California because they are both well-documented (using records from GBIF and Calflora 2021, respectively).

Defining the historic native range limit

D. graveolens' historic native distribution is centered around the Mediterranean Basin, extending eastward to the Middle East and NW-India, and northward into central France (Tutin et al. 1976, Brullo and De Marco 2000). The first records of a large-scale northward range expansion of *D. graveolens* appear for the 1950s in northern France, initially associated with salt mines and followed by abundant spread along roads (Wagenitz 1966, Ciardo and Delarze 2005, Parent 2011). We chose 1901-1930 as the pre-expansion time window for our study, which matches the earliest available information about *D. graveolens*' distribution in floras of France (Coste 1903,

Rouy 1903, Bonnier and Layens 1909) and the Balkan Peninsula (Hayek and Markgraf 1931), as well as the earliest monthly climate data (see next section). We used the botanical literature, dated species occurrences, and online databases to define a hypothesized *historic native range limit* pre-expansion (Supporting Information). We considered administrative regions where *D. graveolens* is reported as a native species to be part of the historic native range (e.g., Flora Europaea, Tutin et al. 1976, and Euro+Med PlantBase, von Raab-Straube 2021), refining country-level data using other data sources.

Environmental predictors

Monthly temperature and precipitation data were compiled from the Climatic Research Unit (CRU TS4.04, Harris et al. 2020) for 1901-1930 (past) and 1990-2019 (present), and used to calculate all 19 WORLDCLIM variables (Fick and Hijmans 2017) for each time period (dismo package; Hijmans et al. 2017). In addition, we calculated the average total number of frost days for September-December (hereafter “frost”) for the same data sets. We selected 6 predictors (Table 1) based on the biology of *D. graveolens*, the Mediterranean and temperate climates characteristic of the expanded native range, and criteria limiting multicollinearity among variables: a pairwise Pearson correlation of 0.75 or less and a Variance Inflation Factor (usdm package, Naimi et al. 2014) below 5 (as recommended by Guisan et al. 2017). *D. graveolens* is a late-season annual plant, establishing a rosette in late spring and fruiting in fall (Brownsey et al. 2013b), with earlier phenology occurring at higher latitudes (Lustenhouwer et al. 2018). In early life stages, precipitation is key to the growth of a tap root (Brownsey et al. 2013a), whereas plants are sensitive to cold and especially frost later in the year (Parsons and Cuthbertson 2001), when the end of the growing season constrains plant fitness (Lustenhouwer et al. 2018). We

considered climate variables representing temperature, precipitation, and their variability. Collinearity was evaluated over the entire Eurasian Holarctic. Based on *D. graveolens*' biology, we discarded annual temperature and precipitation in favor of frost days during the reproductive period and precipitation in the driest and warmest quarters. Temperature of these quarters was highly correlated with the other selected variables and excluded.

Modeling approach

To combine climate and occurrence data, we scaled the latter down to the same resolution with one record per grid cell (0.5° latitude and longitude, corresponding to ca. 55 by 55 km). Cells containing occurrence records but no climate data (primarily covering sea rather than land, at coastlines or islands) were excluded. We set up two primary datasets, past and present, for our native range analyses covering the same Holarctic study region. The past dataset (representing the historic native range) consisted of climate data for the period 1901-1930 and all occurrence records located within the historic native range limit (n=399), assuming that occurrence locations represent suitable habitat for *D. graveolens* regardless of the date of observation. The present dataset (representing the expanded native range) consisted of climate data for the period 1990-2019 and the complete set of occurrence records (n=746). We used present-day climate data for the invaded range datasets. The Australia dataset contained all GBIF occurrences on the continent. The California dataset covered all of North America in spatial extent but occurrence data for California only, to focus on the west coast invasion. All analyses were conducted in R v4.0.0 (R Core Team 2020), using code adapted from Di Cola et al. (2017), Guisan et al. (2017), and Smith (2020a).

Niches in environmental space

To quantify niche dynamics during range expansion following the COUE framework (Guisan et al. 2014), we applied the workflow developed by Broennimann et al. (2012), available in the ecospat R package (Di Cola et al. 2017, Broennimann et al. 2020). This approach evaluates niches in environmental space, which is defined by conducting a principal component analysis (PCA) for all environmental variables in both study regions under comparison. Niches are estimated by applying a kernel smoother function to the density of species occurrences from each range in gridded environmental space along the first two PCA axes. Indices of niche change are calculated exclusively for environments that are available in both study regions (using the 90th percentile to exclude marginal environments), because shifts to and from nonanalog climates do not represent shifts in the fundamental niche (Guisan et al. 2014). *Niche stability* is defined as the proportion of occurrences in the new niche that overlap in environmental space with the native niche, while *niche expansion* (1-stability) is the proportion of occurrences in the new niche that are located in novel environments. Finally, *niche unfilling* quantifies environmental space that is occupied in the native range but that has not been filled in the new range (yet). It is calculated for the native occurrences as the proportion located in climate conditions that are unoccupied (but available) in the new range (Di Cola et al. 2017). Overall *niche overlap* is measured by Schoener's *D* (Schoener 1970) and used to test for niche conservatism during range expansion with two different tests (Warren et al. 2008, Broennimann et al. 2012). The niche equivalency test randomly reallocates occurrences between the two niches, creating a null distribution of *D* values based on 100 permutations to test whether the niches are identical (conducting one-sided tests asking if the observed *D* is greater or lower than expected by chance). The niche similarity test evaluates whether the two niches are more or less similar to each other than to other niches

selected at random from the study area (shifting niches across both time periods for the native study area, but in the invaded study area only for Australia and California). We applied the above workflow to niche changes between (i) the past and present dataset (native range expansion), (ii) the past dataset and each invaded range, and (iii) the present dataset and each invaded range.

Projections in geographic space

To project niche changes in geographic space, we fit Maxent species distribution models (Phillips et al. 2006) to the past dataset (Past Model) and present dataset (Present Model). Maxent performs well for presence-only data under a range of sampling scenarios (Grimmett et al. 2020). Because the geographic availability of our native range occurrence data was highly concentrated in Western Europe, we used 3468 target background sites of taxonomically related species to correct for bias in sampling effort (Phillips et al. 2009, Supporting Information). Models were fit using the maxnet package in R (Phillips 2017, Phillips et al. 2017). We first tuned the Past Model, using the trainMaxnet function (enmSdm package, Smith 2020b) to select the optimal combination of features (starting with all classes) and regularization parameters (β of 0.5 and 1 to 10). The best model (lowest AIC) contained linear, quadratic and product features with $\beta=0.5$. We fit the Present Model using the same features and regularization. To ask whether *D. graveolens* simply tracked optimal climate conditions or expanded its native range beyond that, we created three model projections: the Past Model on the past and present climate, and the Present Model on the present climate. To evaluate model performance, we partitioned the past and present datasets randomly into training and test data using 5 k-folds. We computed AUC (dismo, Hijmans et al. 2017) and the Continuous Boyce Index (CBI; enmSdm, Smith 2020b) for each k-fold and calculated the mean and standard deviation across models. To project areas at

potential risk of invasion in California and Australia, we applied a Minimum Presence Threshold (the lowest habitat suitability at which *D. graveolens* is already present in the invaded range). We then compared projections generated by the Past and Present model for each invaded range.

Results

Over the course of less than a century, *D. graveolens* has shifted its native range limit northward by nearly 7 degrees latitude. During this range expansion, the climate niche expanded by 5% to include more temperate environments with lower diurnal range and precipitation seasonality (bio2, bio15), increased precipitation in the driest and warmest quarters (bio17, bio18), and increased temperature seasonality (bio4) and fall frost (Fig. 1a,b). Niche overlap (Schoener's $D = 0.71$) of the historic and expanded native niche was significantly lower than expected by chance (niche equivalency test; Fig. 1c, Table 2), indicating a niche shift during range expansion. Nonetheless, the two niches were more similar to each other than to randomly selected niches in the study area (niche similarity test; Fig. 1d, Table 2). Niche expansion was not driven by climate change between the past and present period, which happened in a different direction in environmental space (reduced frost and temperature seasonality; Fig. 1a).

In line with this climate niche expansion, we found that *D. graveolens* in Eurasia has expanded its geographic range well beyond the extent sufficient to track climate change (Fig. 2; Supporting Information). The Past Model, fit to the historic climate and occurrences (Supporting Information), predicts suitable habitat for *D. graveolens* around the Mediterranean Basin and into central France as expected (Fig. 2a). Model AUC was 0.89 ± 0.01 , indicating good to excellent performance (Araújo et al. 2005). Projecting this model onto the present climate (Fig. 2b), we

found a minor northward shift in favorable conditions, particularly adjacent to the original northern range limit in France. However, the observed range expansion of *D. graveolens* extended much further northward and eastward (Fig. 2c). The Present Model, fit to the present climate and occurrences (Supporting Information), predicts a much wider distribution in Europe (Fig. 2d), outperforming the Past Model especially when predicting the actual probability of occurrence in the present (CBI of 0.93 and 0.61, respectively; Table 3).

The invasions in California and Australia exhibited contrasting niche dynamics, consistent with their difference in invader residence time. In California, only a small subset of the climate conditions in the native niche are already occupied (niche unfilling was 93% at the scale of North America; Fig. 3d, Table 2). In contrast, the Australian invasion has already spread into most areas that show similar climatic conditions to the native range (unfilling 6%; Fig. 3a, Table 2). These contrasting results were reflected in the niche equivalency test, which showed that the California niche was less similar to the historic native range than expected by chance, while the Australian niche was more similar than expected (Table 2). We found near-complete niche stability in both invasions, meaning that invasive populations occur almost exclusively in climate conditions that also existed in the historic native range. Accordingly, niche expansion was low (Table 2). Niche conservatism could not be rejected in the niche similarity test for either invasion, indicating that it cannot be ruled out that any niche differentiation between native and exotic ranges was driven by the availability of environments in the exotic ranges.

Niche change indices were similar for both invasions when including the native range expansion (Table 2). Even though the peak of native occurrences shifted toward more temperate climates

(shading in Fig. 3e), California niche unfilling remained stable because the majority of native occurrences already occurred outside the invaded climate space. Of the newly invadable climate conditions, most are absent in Australia (Fig. 3b), but present in North America (Fig. 3e). Combining projections of the Past and Present Maxent models onto Australia and California revealed additional areas that would be at risk of invasion if niche shifts were to happen as in the native range. However, neither invasion has yet advanced into areas solely included by the Present Model (Fig. 3c, 3f).

Discussion

As many native species are shifting their ranges to track climate change, the ecological and evolutionary drivers of range expansion have become a key focus of global change research (Nadeau and Urban 2019). Ecological studies of native range shifts have found varying degrees to which species keep up with shifting climate isotherms (Chen et al. 2011, Lenoir et al. 2020), including some species that outpace climate warming. Two studies using a similar approach to ours, comparing historic and current ranges using ENMs, found incomplete climate tracking (*Ilex aquifolium*, Walther et al. 2005) or range contractions rather than expansions (montane rodents, Pardi et al. 2020). In contrast, our results show that *D. graveolens* has undergone an extensive northward expansion of its native range, beyond what would be expected based on climate tracking alone.

At the start of the native range expansion, the first records of *D. graveolens* north of the historic range limit in France (GBIF.org 2020) match the availability of new suitable habitat there with climate change (Fig. 2b). Theory predicts that rapid evolution of both local adaptation and

increased dispersal during range expansion could cause populations to spread beyond shifting climate isotherms, while expanding their fundamental niche to include colder climates (Kubisch et al. 2013). Our results are consistent with such a scenario, where adaptation to climate conditions at northern latitudes (Fig. 1) facilitated further spread of *D. graveolens* (Fig. 2c). Niche expansion (5.5%, following Broennimann et al. 2012) was high relative to comparative studies of niche shifts during invasion using the same metrics, falling in the 78th percentile of expansion estimates by Petitpierre et al. (2012, n = 50 plant species), and the 60th percentile of Liu et al. (2020, n = 211 plant species with COUE estimates). Niche expansion was low compared to results in Early & Sax (2014). These authors found much higher niche expansion overall than Petitpierre et al., which they attributed life history differences between the study species; Early & Sax considered endemic species with small native ranges while Petitpierre et al. studied weedy species that were widely distributed in their native range, more similar to *D. graveolens*.

We found little evidence for niche expansion in the invaded range. Australia and California differed strongly in niche unfilling, illustrating the importance of invader residence time in invasion risk assessment (Wilson et al. 2007). Although the California invasion appears to be in much earlier stages with further dispersal expected, both invasive niches almost exclusively cover climatic conditions that are also present in the native niche (high stability), a pattern known as climate matching, which has been found for many successful invasive species (Hayes and Barry 2008). Interestingly, despite its longer history, the Australian niche barely expands beyond the native niche, suggesting niche conservatism. Incorporating the native range expansion into projections of niche change and invasion risk adds newly invadable

climates/habitat especially in North America (Fig. 3). However, given that neither invasion has yet spread into these areas, it remains an open question whether any similar niche evolution can be expected in the invaded ranges in the future. The strong overlap in climate conditions occupied in the historic native range and both exotic ranges does suggest that invasive populations originated from a Mediterranean part of the native range.

Limitations

Any niche modeling study is constrained by the available data. Although the native and invaded distributions of *D. graveolens* are relatively well-documented, occurrence records do contain temporal and spatial biases that may have affected our results. Because the majority of our occurrence data was reported in recent decades, we included all occurrences south of the original range limit in the historic native range, regardless of the date they were reported. It is possible that past climate conditions at these locations were less favorable for *D. graveolens*. However, because our study is focused on a northward range expansion tracking climate change, and the historic native range now represents the trailing edge of the distribution, our assumption to treat all occurrences as historical presences should underestimate the niche shift during range expansion and therefore represents a conservative approach. To address the spatial bias in our data, we employed the target background record approach to reflect sampling effort across the study area. This solution was a great improvement over randomly chosen background points (which resulted in overfitting to climate areas with high sampling effort), but was still not optimal given the low number of target background points available compared to Maxent's standard of 10,000. However, at our spatial resolution (0.5°) even near 215,000 target records from 296 species covered only 3468 cells across the entire study area (Supporting Information).

Higher-resolution climate data would allow for more background points (Merow et al. 2013) but was not available for the past time period of interest.

Niche expansion as quantified in this study can represent either a change in the realized niche due to lifted biotic or dispersal constraints, or be caused by evolution of the fundamental niche. *D. graveolens* has very high spread potential due to a combination of an annual life history, wind-dispersed seeds and the production of tens of thousands of seeds per plant. No historic barriers to dispersal are apparent in the native range. Moreover, *D. graveolens* has a typical ruderal life history and has expanded its native range primarily along roadsides, with limited biotic interactions with other species. Finally, previous work has demonstrated that rapid evolution of earlier phenology increased plant fitness in northern leading-edge populations (Lustenhouver et al. 2018). We therefore argue that evolution of the fundamental niche is the most plausible explanation for the observed climate niche expansion.

Broader implications

Our finding of greater niche expansion during native range expansion than during invasion contradicts hypotheses in the literature that niche stasis should be more pronounced in the native range (Pearman et al. 2008, Wiens et al. 2019). Rather than having a maladaptive swamping effect, gene flow in the native range brought in genetic variation from the northern end of existing latitudinal clines that was adaptive in northern climates (Lustenhouver et al. 2018). In order to definitively assess the evolutionary potential of *D. graveolens* in California and predict whether this invasion will proceed into areas forecasted by the Present Model (Fig. 3c), empirical studies comparing plants of native and invasive origin will be necessary. Nonetheless, our study

supports calls to limit multiple introductions of invasive species, even if they are widespread already (Smith et al. 2020), because the introduction of genotypes from northern Europe to California would put new areas at risk of invasion (Fig. 3e,f).

In conclusion, our results suggest that climate change may act as a catalyst for range expansion and subsequent climate niche evolution in plants. The generality of this phenomenon for other species will depend on their evolutionary potential (generation time, heritable genetic diversity), range-limiting factors, and dispersal ability (Catullo et al. 2015). Recent work on invertebrates suggests that range expansion can promote increased thermal and diet niche breadth at the range edge in many species (Lancaster 2016, 2020). We encourage future studies validating native range shift projections with observed spread (e.g., Araújo et al. 2005), to examine whether climate niche evolution during native range expansion is common and causes populations to spread further than expected under climate tracking. Ultimately, the study of both biological invasions and native species threatened by climate change will benefit from a better understanding of the drivers of niche evolution during range expansion.

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References

- Aitken, S. N. et al. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. - *Evol. Appl.* 1: 95–111.
- Alexander, J. M. and Edwards, P. J. 2010. Limits to the niche and range margins of alien species. - *Oikos* 119: 1377–1386.
- Araújo, M. B. et al. 2005. Validation of species–climate impact models under climate change. - *Glob. Change Biol.* 11: 1504–1513.
- Araújo, M. B. et al. 2011. Climate change threatens European conservation areas. - *Ecol. Lett.* 14: 484–492.
- Atwater, D. Z. et al. 2018. Climatic niche shifts are common in introduced plants. - *Nat. Ecol. Evol.* 2: 34–43.
- Boheemen, L. A. van et al. 2019. Rapid and repeated local adaptation to climate in an invasive plant. - *New Phytol.* 222: 614–627.
- Bonnier, G. and Layens, G. 1909. Flore complète de la France et de la Suisse (comprenant aussi toutes les espèces de Belgique, d’Alsace et de Lorraine). - Librairie générale de l’enseignement.
- Broennimann, O. et al. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. - *Glob. Ecol. Biogeogr.* 21: 481–497.
- Broennimann, O. et al. 2020. ecospat: Spatial Ecology Miscellaneous Methods. R package version 3.1.
- Brownsey, R. et al. 2013a. Seed and Germination Biology of *Dittrichia graveolens* (Stinkwort). - *Invasive Plant Sci. Manag.* 6: 371–380.
- Brownsey, R. et al. 2013b. Stinkwort is rapidly expanding its range in California. - *Calif. Agric.* 67: 110–115.
- Brullo, S. and De Marco, G. 2000. Taxonomical revision of the genus *Dittrichia* (Asteraceae). - *Port. Acta Biol.* 19: 341–354.
- BSBI 2020. Botanical Society of Britain and Ireland Distribution Database. Records for *Dittrichia graveolens* accessed June 5, 2020.
- Bush, A. et al. 2016. Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. - *Ecol. Lett.* 19: 1468–1478.
- Calflora 2021. Calflora: Information on California plants for education, research and conservation [web application]. - The Calflora Database [a non-profit organization].

- 468 Catullo, R. A. et al. 2015. Extending spatial modelling of climate change responses beyond the
469 realized niche: estimating, and accommodating, physiological limits and adaptive
470 evolution. - Glob. Ecol. Biogeogr. 24: 1192–1202.
- 471 Chen, I.-C. et al. 2011. Rapid range shifts of species associated with high levels of climate
472 warming. - Science 333: 1024–1026.
- 473 Chuang, A. and Peterson, C. R. 2016. Expanding population edges: theories, traits, and trade-
474 offs. - Glob. Change Biol. 22: 494–512.
- 475 Ciardo, F. and Delarze, R. 2005. Observations floristiques sur l'autoroute lémanique: espèces
476 nouvelles, halophiles et rares. - Saussurea Travaux Société Bot. Genève 35: 83–89.
- 477 Colautti, R. I. and Barrett, S. C. H. 2013. Rapid adaptation to climate facilitates range expansion
478 of an invasive plant. - Science 342: 364–366.
- 479 Colautti, R. I. and Lau, J. A. 2015. Contemporary evolution during invasion: evidence for
480 differentiation, natural selection, and local adaptation. - Mol. Ecol. 24: 1999–2017.
- 481 Corlett, R. T. and Westcott, D. A. 2013. Will plant movements keep up with climate change? -
482 Trends Ecol. Evol. 28: 482–488.
- 483 Coste, H. 1903. Flore descriptive et illustrée de la France, de la Corse, et des contrées
484 limitrophes. - P. Klincksieck.
- 485 Cox, B. 2001. The biogeographic regions reconsidered. - J. Biogeogr. 28: 511–523.
- 486 Di Cola, V. et al. 2017. ecospat: an R package to support spatial analyses and modeling of
487 species niches and distributions. - Ecography 40: 774–787.
- 488 Diamond, S. E. 2018. Contemporary climate-driven range shifts: Putting evolution back on the
489 table. - Funct. Ecol. 32: 1652–1665.
- 490 Dlugosch, K. M. and Parker, I. M. 2008a. Invading populations of an ornamental shrub show
491 rapid life history evolution despite genetic bottlenecks. - Ecol. Lett. 11: 701–709.
- 492 Dlugosch, K. M. and Parker, I. M. 2008b. Founding events in species invasions: genetic
493 variation, adaptive evolution, and the role of multiple introductions. - Mol. Ecol. 17: 431–
494 449.
- 495 Dudaniec, R. Y. et al. 2018. Signatures of local adaptation along environmental gradients in a
496 range-expanding damselfly (*Ischnura elegans*). - Mol. Ecol. 27: 2576–2593.
- 497 Early, R. and Sax, D. F. 2014. Climatic niche shifts between species' native and naturalized
498 ranges raise concern for ecological forecasts during invasions and climate change. - Glob.
499 Ecol. Biogeogr. 23: 1356–1365.

500 Elith, J. and Leathwick, J. R. 2009. Species Distribution Models: Ecological Explanation and
501 Prediction Across Space and Time. - Annu. Rev. Ecol. Evol. Syst. 40: 677–697.

502 Fick, S. E. and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces
503 for global land areas. - Int. J. Climatol. 37: 4302–4315.

504 FloraWeb 2013. *Dittrichia graveolens* in FloraWeb: Daten und Informationen zu Wildpflanzen
505 und zur Vegetation Deutschlands.

506 GBIF.org 2020. GBIF Occurrence Download for *Dittrichia graveolens* (L.) Greuter,
507 <https://doi.org/10.15468/dl.s0qcs0>.

508 Grimmer, L. et al. 2020. Presence-only species distribution models are sensitive to sample
509 prevalence: Evaluating models using spatial prediction stability and accuracy metrics. -
510 Ecol. Model. 431: 109194.

511 2017. 6. Environmental Predictors: Issues of Processing and Selection. - In: Guisan, A. et al.
512 (eds), Habitat Suitability and Distribution Models: With Applications in R. Ecology,
513 Biodiversity and Conservation. Cambridge University Press, pp. 61–109.

514 Guisan, A. 2017. Habitat suitability and distribution models, with applications in R. - Cambridge
515 University Press.

516 Guisan, A. et al. 2014. Unifying niche shift studies: insights from biological invasions. - Trends
517 Ecol. Evol. 29: 260–269.

518 Harris, I. et al. 2020. Version 4 of the CRU TS monthly high-resolution gridded multivariate
519 climate dataset. - Sci. Data 7: 109.

520 Hayek, A. and Markgraf, F. 1931. Prodrum florae peninsulae balcanica / A. Hayek; F.
521 Markgraf; 2: Dicotyledoneae sympetalae.

522 Hayes, K. R. and Barry, S. C. 2008. Are there any consistent predictors of invasion success? -
523 Biol. Invasions 10: 483–506.

524 Hijmans, R. J. et al. 2017. dismo: Species Distribution Modeling.

525 Hill, M. P. et al. 2013. A predicted niche shift corresponds with increased thermal resistance in
526 an invasive mite, *Halotydeus destructor*. - Glob. Ecol. Biogeogr. 22: 942–951.

527 Hoffmann, A. A. and Sgrò, C. M. 2011. Climate change and evolutionary adaptation. - Nature
528 470: 479–485.

529 iNaturalist 2020. Available from <https://www.inaturalist.org>.

530 Info Flora 2020. *Dittrichia graveolens* in: Info Flora, the National Data and Information Center
531 on the Swiss Flora. www.infoflora.ch.

532 Jakob, S. S. et al. 2010. Population demography influences climatic niche evolution: evidence
533 from diploid American *Hordeum* species (Poaceae). - *Mol. Ecol.* 19: 1423–1438.

534 Kearney, M. et al. 2009. Integrating biophysical models and evolutionary theory to predict
535 climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. -
536 *Funct. Ecol.* 23: 528–538.

537 Kottler, E. J. et al. 2021. Draining the swamping hypothesis: little evidence that gene flow
538 reduces fitness at range edges. - *Trends Ecol. Evol.* 36: 533–544.

539 Kubisch, A. et al. 2013. Predicting range shifts under global change: the balance between local
540 adaptation and dispersal. - *Ecography* 36: 873–882.

541 Lancaster, L. T. 2016. Widespread range expansions shape latitudinal variation in insect thermal
542 limits. - *Nat. Clim. Change* 6: 618–621.

543 Lancaster, L. T. 2020. Host use diversification during range shifts shapes global variation in
544 Lepidopteran dietary breadth. - *Nat. Ecol. Evol.*: 1–7.

545 Lancaster, L. T. et al. 2015. Latitudinal shift in thermal niche breadth results from thermal
546 release during a climate-mediated range expansion. - *J. Biogeogr.* 42: 1953–1963.

547 Lee-Yaw, J. A. et al. 2019. Range shifts and local adaptation: integrating data and theory towards
548 a new understanding of species' distributions in the Anthropocene. - *New Phytol.* 221:
549 644–647.

550 Lenoir, J. et al. 2020. Species better track climate warming in the oceans than on land. - *Nat.*
551 *Ecol. Evol.*: 1–16.

552 Liu, C. et al. 2020. Most invasive species largely conserve their climatic niche. - *Proc. Natl.*
553 *Acad. Sci.* 117: 23643–23651.

554 Lustenhouwer, N. et al. 2018. Rapid evolution of phenology during range expansion with recent
555 climate change. - *Glob. Change Biol.* 24: e534–e544.

556 Martínez-Meyer, E. et al. 2004. Ecological niches as stable distributional constraints on mammal
557 species, with implications for Pleistocene extinctions and climate change projections for
558 biodiversity. - *Glob. Ecol. Biogeogr.* 13: 305–314.

559 Merow, C. et al. 2013. A practical guide to MaxEnt for modeling species' distributions: what it
560 does, and why inputs and settings matter. - *Ecography* 36: 1058–1069.

561 Moran, E. V. and Alexander, J. M. 2014. Evolutionary responses to global change: lessons from
562 invasive species. - *Ecol. Lett.* 17: 637–649.

563 Nadeau, C. P. and Urban, M. C. 2019. Eco-evolution on the edge during climate change. -
564 *Ecography* in press.

565 Naimi, B. et al. 2014. Where is positional uncertainty a problem for species distribution
566 modelling? - *Ecography* 37: 191–203.

567 Nikolić, T. 2015. Flora Croatica Database, <http://hirc.botanic.hr/fcd>.

568 Nogués-Bravo, D. et al. 2018. Cracking the Code of Biodiversity Responses to Past Climate
569 Change. - *Trends Ecol. Evol.* 33: 765–776.

570 Pardi, M. I. et al. 2020. Testing climate tracking of montane rodent distributions over the past
571 century within the Great Basin ecoregion. - *Glob. Ecol. Conserv.* 24: e01238.

572 Parent, G. H. 2011. Etudes ecologiques et chorologiques sur la flore Lorraine. Note 26: quelques
573 taxons nouveaux ou meconnus de Lorraine française. Données rassemblées de 1993 à
574 2005. - *Inst. Grand-ducal Luxemb. Sect. Sci. Nat. Phys. Mathématiques Nouv. Sér.* 46:
575 5–40.

576 Parsons, W. T. and Cuthbertson, E. G. 2001. Stinkwort. - In: *Noxious Weeds of Australia*.
577 Second Edition. Csiro Publishing, pp. 281–283.

578 Pearman, P. B. et al. 2008. Niche dynamics in space and time. - *Trends Ecol. Evol.* 23: 149–158.

579 Petitpierre, B. et al. 2012. Climatic niche shifts are rare among terrestrial plant invaders. -
580 *Science* 335: 1344–1348.

581 Phillips, S. 2017. Maxnet: fitting “maxent” species distribution models with “glmnet”. R package
582 version 0.1.2.

583 Phillips, S. J. et al. 2006. Maximum entropy modeling of species geographic distributions. -
584 *Ecol. Model.* 190: 231–259.

585 Phillips, S. J. et al. 2009. Sample selection bias and presence-only distribution models:
586 implications for background and pseudo-absence data. - *Ecol. Appl.* 19: 181–197.

587 Phillips, S. J. et al. 2017. Opening the black box: an open-source release of Maxent. - *Ecography*
588 40: 887–893.

589 Polechová, J. and Barton, N. H. 2015. Limits to adaptation along environmental gradients. -
590 *Proc. Natl. Acad. Sci.* 112: 6401–6406.

591 Preston, R. E. 1997. *Dittrichia graveolens* (Asteraceae), new to the California weed flora. -
592 *Madroño* 44: 200–203.

593 QGIS Development Team 2019. QGIS Geographic Information System. - Open Source
594 Geospatial Foundation.

595 R Core Team 2020. R: A language and environment for statistical computing. - R Foundation for
596 Statistical Computing.

597 Rios, N. E. 2020. GEOLocate. A platform for georeferencing natural history collections data.
598 <https://www.geo-locate.org/>.

599 Rouy, G. 1903. XLIV. Rubiacées - XLVIII. Composées. - In: Flore de France, ou description des
600 plantes qui croissent spontanément en France, en Corse et en Alsace-Lorraine. Deslis, pp.
601 205–206.

602 Saikkonen, K. et al. 2012. Climate change-driven species' range shifts filtered by
603 photoperiodism. - Nat. Clim. Change 2: 239–242.

604 Santilli, L. et al. 2021. First record of *Dittrichia graveolens* (Asteraceae, Inuleae) in Chile. -
605 Darwiniana Nueva Ser.: 31–38.

606 Schoener, T. W. 1970. Nonsynchronous Spatial Overlap of Lizards in Patchy Habitats. - Ecology
607 51: 408–418.

608 Smith, A. B. 2020a. Best practices in species distribution modeling: a workshop in R. Available
609 at <http://www.earthskysea.org/>.

610 Smith, A. B. 2020b. enmSdm: Tools for modeling niches and distributions of species. R package
611 version 0.5.2.9.

612 Smith, A. L. et al. 2020. Global gene flow releases invasive plants from environmental
613 constraints on genetic diversity. - Proc. Natl. Acad. Sci. 117: 4218–4227.

614 Spence, A. R. and Tingley, M. W. 2020. The challenge of novel abiotic conditions for species
615 undergoing climate-induced range shifts. - Ecography in press.

616 Taulavuori, K. et al. 2010. Growth responses of trees to arctic light environment. - In: Lüttge, U.
617 et al. (eds), Progress in Botany 71. Progress in Botany. Springer, pp. 157–168.

618 Tutin, T. G. et al. 1976. Flora Europaea. Volume 4. Plantaginaceae to Compositae (and
619 Rubiaceae). - Cambridge University Press.

620 Urban, M. C. et al. 2016. Improving the forecast for biodiversity under climate change. - Science
621 353: aad8466.

622 USDA 2013. Weed Risk Assessment for *Dittrichia graveolens* (L.) Greuter (Asteraceae) –
623 Stinkwort.

624 Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate
625 change. - Proc. R. Soc. B Biol. Sci. 275: 649–659.

626 2021. *Dittrichia graveolens* (E von Raab-Straube, Ed.). - EuroMed PlantBase

627 Wagenitz, G. 1966. Compositae I: Allgemeiner Teil, Eupatorium - Achillea. - In: Illustrierte
628 Flora von Mitteleuropa. Parey, in press.

629 Walther, G.-R. et al. 2005. An ecological ‘footprint’ of climate change. - Proc. R. Soc. B Biol.
630 Sci. 272: 1427–1432.

631 Warren, D. L. et al. 2008. Environmental Niche Equivalency Versus Conservatism: Quantitative
632 Approaches to Niche Evolution. - Evolution 62: 2868–2883.

633 Wiens, J. J. et al. 2019. Rapid niche shifts in introduced species can be a million times faster than
634 changes among native species and ten times faster than climate change. - J. Biogeogr. 46:
635 2115–2125.

636 Wilson, J. R. U. et al. 2007. Residence time and potential range: crucial considerations in
637 modelling plant invasions. - Divers. Distrib. 13: 11–22.

638 Zając, A. and Zając, M. 2019. Distribution atlas of vascular plants in Poland: appendix. -
639 Institute of Botany, Jagiellonian University.

640

Figures

Figure 1 Niche shift during native range expansion, comparing the past (1901-1930) and present (1990-2019) datasets; (a) past and present niche in environmental space, with colors indicating niche stability (purple), unfilling (orange) and expansion (blue), and the white arrow showing the niche centroid shift. Dark shading shows the density of occurrences in the historic range. Lines represent the climate of the Eurasian Holarctic in the past (orange) and present (blue), using 100% (solid) and 90% (dashed) of available climates. The black arrow indicates the climate centroid shift between past and present. (b) principal component analysis of the entire environmental space, with axes explaining 41.6% (x) and 29.0% (y) of variation. Arrows show environmental predictors as defined in Table 1. (c, d) niche equivalency and niche similarity test, with histograms showing null distributions and diamonds marking observed niche overlap.

Figure 2 Maxent habitat suitability results for (a) the Past Model (fit to the past climate and historic native range occurrences) projected onto the past climate (1901-1930); (b) the Past Model projected onto the present climate (1990-2019), indicating expected range expansion with climate change; (c) the same projection with observed occurrences in the present, and (d) the Present Model (fit to the present climate and all occurrences) projected onto the present climate. Historic native range limit represented by the black line, and species occurrence records in the historic (a,b) and expanded (c,d) native range by dots. Axes display degrees longitude (x) and latitude (y). Projections for the entire study area available in the Supporting Information.

Figure 3 Niche shift during invasion in Australia (a,b) and California (d,e), using the past native (a,d) and present native (b,e) niche and climate as a reference. Colors indicate niche stability, unfilling and expansion as in Fig. 1, with lines representing the climate of the native (orange) and exotic (blue) study area. Shading shows the density of occurrences from the historic (a,d) and expanded (b,e) native range in environmental space. Panels c and f show areas at risk of invasion as projected by the Past and Present Model, with cells shaded from dark to light as follows: cell included in the Past Model only, in both models, in the Present Model only, or in neither model. Points indicate observation records for *D. graveolens* in Australia (c) and California (f).

Tables

Table 1 Environmental predictors included in this study, with minimum (min), median (med)

and maximum (max) values across all pixels in each study area. Data from CRU TS4.04.

Predictor		Eurasian Holarctic (1901-1930)			Eurasian Holarctic (1990-2019)			North America			Australia		
		min	med	max	min	med	max	min	med	max	min	med	max
bio2	mean diurnal range (°C)	4.2	10.5	18.0	4.4	10.3	18.1	4.6	10.5	20.8	6.7	14.4	16.5
bio4	temperature seasonality (100xSD, °C)	289	1288	2448	295	1255	2365	108	1171	1705	113	545	679
bio15	precipitation seasonality (CV, mm)	21	61	173	23	63	176	19	63	183	21	94	162
bio17	precipitation driest quarter (mm)	0	34	470	0	35	503	0	44	403	0	18	236
bio18	precipitation warmest quarter (mm)	0	163	1383	0	169	1248	1	182	930	24	140	1032
frost	frost days Sep-Dec (count)	0	85	180	0	79	177	0	91	174	0	4	82

Table 2 Niche shift metrics following the COUE framework, calculated using the intersection of the 90th percentile of environmental conditions in each range. Niche equivalency and similarity tests were one-sided, with H₁ indicating the alternative hypothesis used.

Comparison		Niche shift metrics				Niche equivalency test		Niche similarity test	
niche 1	niche 2	D	expansion	stability	unfilling	H ₁	P	H ₁	P
past native	present native	0.71	0.05	0.95	0	lower	0.01**	greater	0.01**
past native	Australia	0.60	0	1.00	0.06	greater	0.01**	greater	0.12
present native	Australia	0.53	0	1.00	0.11	greater	0.01**	greater	0.07
past native	California	0.05	0.01	0.99	0.93	lower	0.01**	greater	0.31
present native	California	0.04	0.03	0.97	0.94	lower	0.01**	greater	0.24

Table 3 Maxent model performance for projections of the Past Model in both time periods, and the projection of the Present Model in the present. All presence and background points were allocated randomly to training and test datasets using 5 k-folds for cross-validation (table shows points per fold). Mean and standard deviation of AUC and CBI are given across the 5 k-folds.

Climate and occurrence data		n presences		n background points		AUC		CBI	
model	projection	training	test	training	test	mean	SD	mean	SD
Past Model	past dataset	319	80	2774	694	0.89	0.01	0.85	0.11
Past Model	present dataset	319	149	2774	694	0.76	0.01	0.61	0.14
Present Model	present dataset	597	149	2774	694	0.81	0.01	0.93	0.04