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

137 method quantifies niches in environmental space and is widely used to study niche dynamics of
138 invasive species. In addition, to explore niche shifts during range expansion in geographic space,
139 we fit species distribution models using maximum entropy modeling (Maxent), which was
140 specifically designed for presence-only data (Phillips et al. 2006). Based on prior evidence for
141 rapid evolution of phenology at the northern range edge (Lustenhouwer et al. 2018), we
142 hypothesized that *D. graveolens*' climate niche expanded during native range expansion in
143 Eurasia. We expected greater niche filling and greater niche expansion in Australia than in
144 California, due to *D. graveolens*' much longer invasion history in the former region. Finally, we
145 hypothesized that forecasting the two invaded distributions based on the newly expanded native
146 range would increase our invasion risk assessment for a wider range of climates and geographic
147 areas.
148

149 **Material and Methods**

150 Data collection

151 *Occurrence data*

152 We compiled presence-only species occurrence data for *Dittrichia graveolens* (L.) Greuter and
153 its nomenclatural synonyms *Inula graveolens* (L.) Desf., *Cupularia graveolens* (L.) Godr. &
154 Gren., and *Erigeron graveolens* (L.). We used the Holarctic Floral Kingdom (Cox 2001) as our
155 study region (split between Eurasia/North Africa for the native range and North America for one
156 of the invaded ranges), to take into account the broadest range of environments available to *D.*
157 *graveolens* in its evolutionary history and facilitate projection of our models to other continents
158 (Merow et al. 2013). This study region also allows for comparison to other studies using the
159 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,

183 Rouy 1903, Bonnier and Layens 1909) and the Balkan Peninsula (Hayek and Markgraf 1931), as
184 well as the earliest monthly climate data (see next section). We used the botanical literature,
185 dated species occurrences, and online databases to define a hypothesized *historic native range*
186 *limit* pre-expansion (Supporting Information). We considered administrative regions where *D.*
187 *graveolens* is reported as a native species to be part of the historic native range (e.g., Flora
188 Europaea, Tutin et al. 1976, and Euro+Med PlantBase, von Raab-Straube 2021), refining
189 country-level data using other data sources.
190
191 *Environmental predictors*
192 Monthly temperature and precipitation data were compiled from the Climatic Research Unit
193 (CRU TS4.04, Harris et al. 2020) for 1901-1930 (past) and 1990-2019 (present), and used to
194 calculate all 19 WORLDCLIM variables (Fick and Hijmans 2017) for each time period (dismo
195 package; Hijmans et al. 2017). In addition, we calculated the average total number of frost days
196 for September-December (hereafter "frost") for the same data sets. We selected 6 predictors
197 (Table 1) based on the biology of *D. graveolens*, the Mediterranean and temperate climates
198 characteristic of the expanded native range, and criteria limiting multicollinearity among
199 variables: a pairwise Pearson correlation of 0.75 or less and a Variance Inflation Factor (usdm
200 package, Naimi et al. 2014) below 5 (as recommended by Guisan et al. 2017). *D. graveolens* is a
201 late-season annual plant, establishing a rosette in late spring and fruiting in fall (Brownsey et al.
202 2013b), with earlier phenology occurring at higher latitudes (Lustenhouwer et al. 2018). In early
203 life stages, precipitation is key to the growth of a tap root (Brownsey et al. 2013a), whereas
204 plants are sensitive to cold and especially frost later in the year (Parsons and Cuthbertson 2001),
205 when the end of the growing season constrains plant fitness (Lustenhouwer et al. 2018). We

206 considered climate variables representing temperature, precipitation, and their variability.
207 Collinearity was evaluated over the entire Eurasian Holarctic. Based on *D. graveolens*' biology,
208 we discarded annual temperature and precipitation in favor of frost days during the reproductive
209 period and precipitation in the driest and warmest quarters. Temperature of these quarters was
210 highly correlated with the other selected variables and excluded.
211
212 Modeling approach
213 To combine climate and occurrence data, we scaled the latter down to the same resolution with
214 one record per grid cell (0.5° latitude and longitude, corresponding to ca. 55 by 55 km). Cells
215 containing occurrence records but no climate data (primarily covering sea rather than land, at
216 coastlines or islands) were excluded. We set up two primary datasets, past and present, for our
217 native range analyses covering the same Holarctic study region. The past dataset (representing
218 the historic native range) consisted of climate data for the period 1901-1930 and all occurrence
219 records located within the historic native range limit (n=399), assuming that occurrence locations
220 represent suitable habitat for *D. graveolens* regardless of the date of observation. The present
221 dataset (representing the expanded native range) consisted of climate data for the period 1990-
222 2019 and the complete set of occurrence records (n=746). We used present-day climate data for
223 the invaded range datasets. The Australia dataset contained all GBIF occurrences on the
224 continent. The California dataset covered all of North America in spatial extent but occurrence
225 data for California only, to focus on the west coast invasion. All analyses were conducted in R
226 v4.0.0 (R Core Team 2020), using code adapted from Di Cola et al. (2017), Guisan et al. (2017),
227 and Smith (2020a).
228

229 *Niches in environmental space*

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

252 selected at random from the study area (shifting niches across both time periods for the native
253 study area, but in the invaded study area only for Australia and California). We applied the above
254 workflow to niche changes between (i) the past and present dataset (native range expansion), (ii)
255 the past dataset and each invaded range, and (iii) the present dataset and each invaded range.
256
257 *Projections in geographic space*
258 To project niche changes in geographic space, we fit Maxent species distribution models
259 (Phillips et al. 2006) to the past dataset (Past Model) and present dataset (Present Model).
260 Maxent performs well for presence-only data under a range of sampling scenarios (Grimmett et
261 al. 2020). Because the geographic availability of our native range occurrence data was highly
262 concentrated in Western Europe, we used 3468 target background sites of taxonomically related
263 species to correct for bias in sampling effort (Phillips et al. 2009, Supporting Information).
264 Models were fit using the maxnet package in R (Phillips 2017, Phillips et al. 2017). We first
265 tuned the Past Model, using the trainMaxnet function (enmSdm package, Smith 2020b) to select
266 the optimal combination of features (starting with all classes) and regularization parameters (β of
267 0.5 and 1 to 10). The best model (lowest AIC) contained linear, quadratic and product features
268 with β=0.5. We fit the Present Model using the same features and regularization. To ask whether
269 *D. graveolens* simply tracked optimal climate conditions or expanded its native range beyond
270 that, we created three model projections: the Past Model on the past and present climate, and the
271 Present Model on the present climate. To evaluate model performance, we partitioned the past
272 and present datasets randomly into training and test data using 5 k-folds. We computed AUC
273 (dismo, Hijmans et al. 2017) and the Continuous Boyce Index (CBI; enmSdm, Smith 2020b) for
274 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

367 climates/habitat especially in North America (Fig. 3). However, given that neither invasion has
368 yet spread into these areas, it remains an open question whether any similar niche evolution can
369 be expected in the invaded ranges in the future. The strong overlap in climate conditions
370 occupied in the historic native range and both exotic ranges does suggest that invasive
371 populations originated from a Mediterranean part of the native range.
372
373 Limitations
374 Any niche modeling study is constrained by the available data. Although the native and invaded
375 distributions of *D. graveolens* are relatively well-documented, occurrence records do contain
376 temporal and spatial biases that may have affected our results. Because the majority of our
377 occurrence data was reported in recent decades, we included all occurrences south of the original
378 range limit in the historic native range, regardless of the date they were reported. It is possible
379 that past climate conditions at these locations were less favorable for *D. graveolens*. However,
380 because our study is focused on a northward range expansion tracking climate change, and the
381 historic native range now represents the trailing edge of the distribution, our assumption to treat
382 all occurrences as historical presences should underestimate the niche shift during range
383 expansion and therefore represents a conservative approach. To address the spatial bias in our
384 data, we employed the target background record approach to reflect sampling effort across the
385 study area. This solution was a great improvement over randomly chosen background points
386 (which resulted in overfitting to climate areas with high sampling effort), but was still not
387 optimal given the low number of target background points available compared to Maxent's
388 standard of 10,000. However, at our spatial resolution (0.5°) even near 215,000 target records
389 from 296 species covered only 3468 cells across the entire study area (Supporting Information).

390 Higher-resolution climate data would allow for more background points (Merow et al. 2013) but
391 was not available for the past time period of interest.
392
393 Niche expansion as quantified in this study can represent either a change in the realized niche
394 due to lifted biotic or dispersal constraints, or be caused by evolution of the fundamental niche.
395 *D. graveolens* has very high spread potential due to a combination of an annual life history,
396 wind-dispersed seeds and the production of tens of thousands of seeds per plant. No historic
397 barriers to dispersal are apparent in the native range. Moreover, *D. graveolens* has a typical
398 ruderal life history and has expanded its native range primarily along roadsides, with limited
399 biotic interactions with other species. Finally, previous work has demonstrated that rapid
400 evolution of earlier phenology increased plant fitness in northern leading-edge populations
401 (Lustenhouwer et al. 2018). We therefore argue that evolution of the fundamental niche is the
402 most plausible explanation for the observed climate niche expansion.
403
404 Broader implications
405 Our finding of greater niche expansion during native range expansion than during invasion
406 contradicts hypotheses in the literature that niche stasis should be more pronounced in the native
407 range (Pearman et al. 2008, Wiens et al. 2019). Rather than having a maladaptive swamping
408 effect, gene flow in the native range brought in genetic variation from the northern end of
409 existing latitudinal clines that was adaptive in northern climates (Lustenhouwer et al. 2018). In
410 order to definitively assess the evolutionary potential of *D. graveolens* in California and predict
411 whether this invasion will proceed into areas forecasted by the Present Model (Fig. 3c), empirical
412 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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Figures

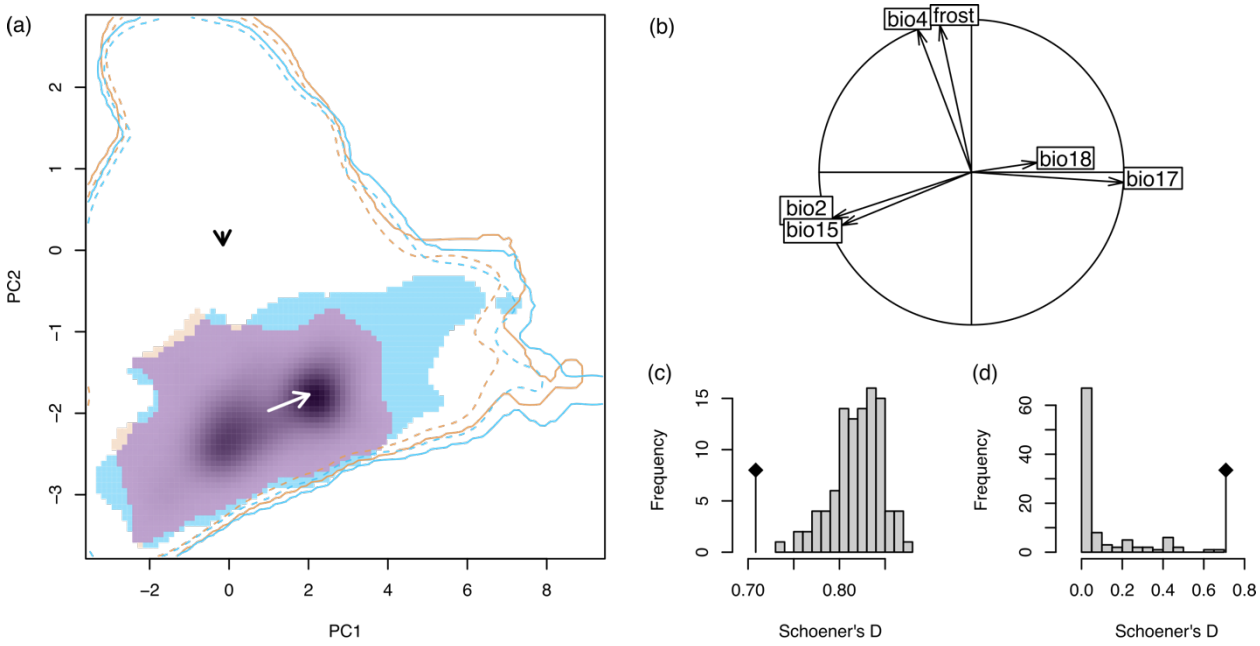

Figure 1 Niche shift during native range expansion, comparing the past (1901-1930) and present (1990-2019) datasets; (a) past and present niche in environmental space, with colors indicating niche stability (purple), unfilling (orange) and expansion (blue), and the white arrow showing the niche centroid 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.

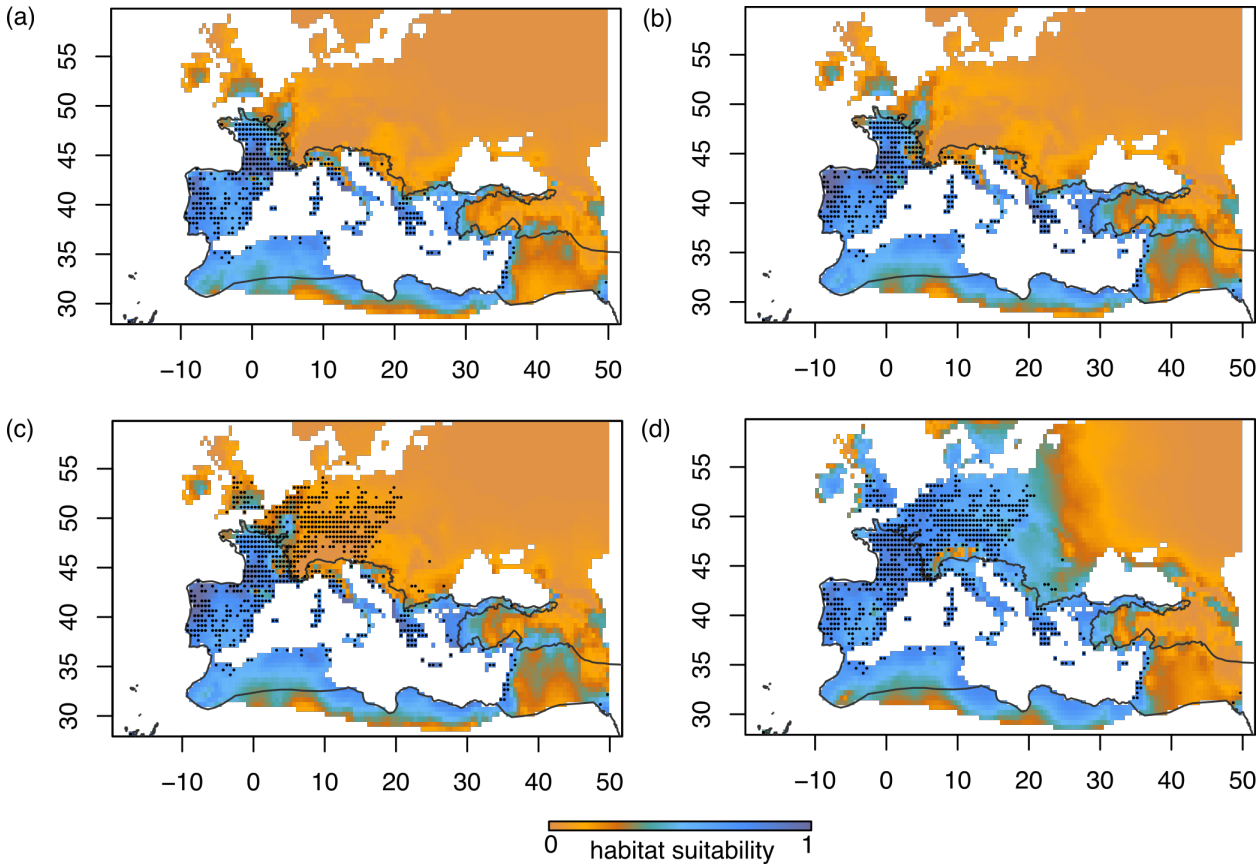

Figure 2 Maxent habitat suitability results for (a) the Past Model (fit to the past climate and historic native range occurrences) projected onto the past climate (1901-1930); (b) the Past Model projected onto the present climate (1990-2019), indicating expected range expansion with climate change; (c) 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.

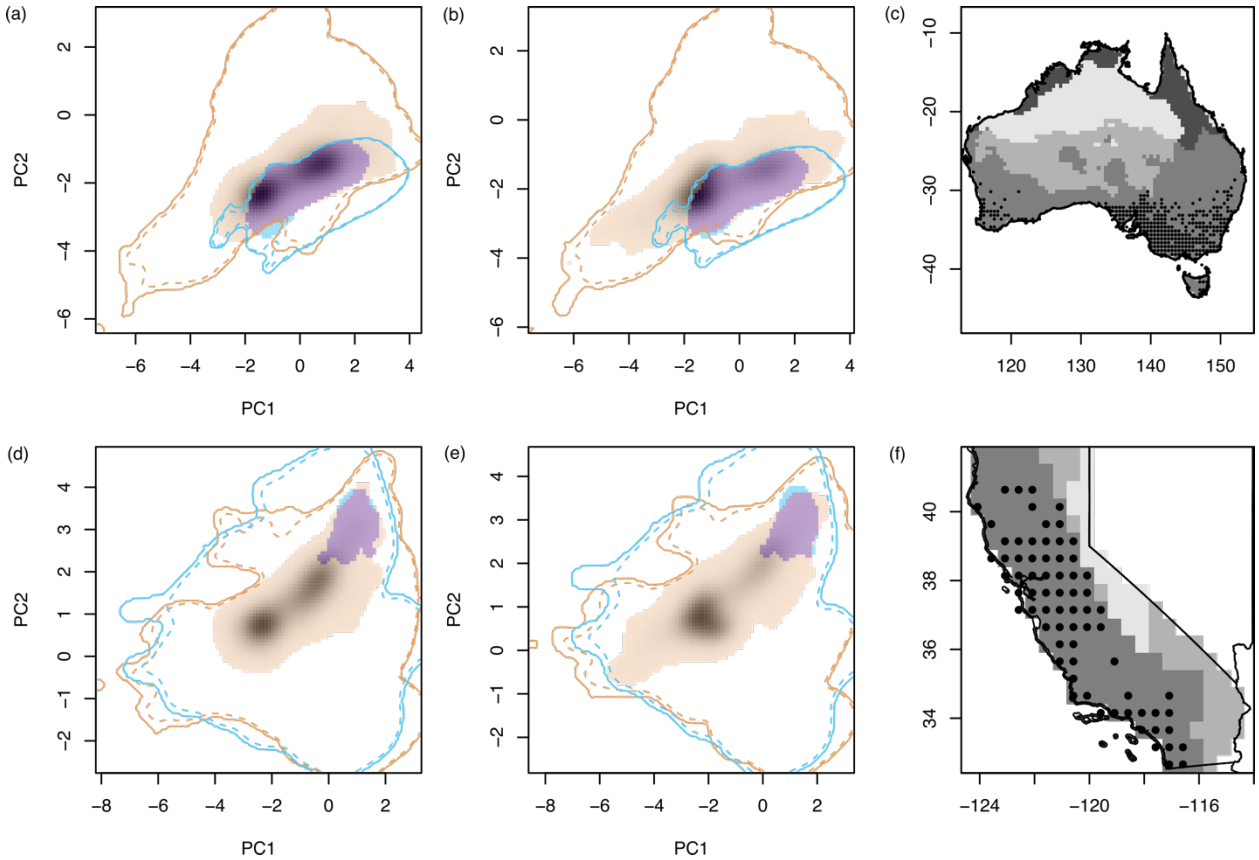

Figure 3 Niche shift during invasion in Australia (a,b) and California (d,e), using the past native (a,d) and present native (b,e) niche and climate as a reference. Colors indicate niche stability, unfilling and expansion as in Fig. 1, with lines representing the climate of the native (orange) and exotic (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 H_1 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