

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

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7

8 **Abstract**

9 Ecological niche models have been instrumental in understanding and forecasting the widespread
10 shifts in species distributions under global change. However, growing evidence of evolution in
11 spreading populations challenges their key assumption of niche conservatism, limiting model
12 transferability in space and time. Climate niche evolution has been studied extensively in
13 invasive species, but may also occur in native populations tracking climate change, when species
14 encounter novel abiotic conditions that vary with latitude. We compared niche shifts during
15 native range expansion and during invasion in *Dittrichia graveolens*, a Mediterranean annual
16 plant species that is currently undergoing both types of spread. We asked whether the species'
17 northward native range expansion in Eurasia matched climate change from 1901-1930 to 1990-
18 2019, or if further range expansion was promoted by niche evolution. In addition, we asked how
19 niche expansion in the native range affected forecasts of two ongoing invasions in Australia and
20 California. We quantified niche shifts in environmental space using the analytical framework of
21 niche centroid shift, overlap, unfilling, and expansion (COUE), and examined associated
22 distribution changes in geographic space using Maximum Entropy modeling. Our results show
23 that *D. graveolens* expanded its native range well beyond what would be sufficient to track

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

31

32 **Keywords**

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

34

35 **Introduction**

36 Forecasting the widespread distribution shifts of both native and invasive species under global
37 change represents one of the major challenges in biodiversity conservation (Urban et al. 2016).

38 The climate niche has become a central concept in modeling efforts to understand species'
39 preferred climate conditions, where such suitable habitat will be present under future climates,
40 and which areas are at risk of invasion on other continents (Elith and Leathwick 2009).

41 Ecological niche models (ENMs; also known as habitat suitability models or species distribution
42 models) are widely used and applied to conservation planning (Araújo et al. 2011). However,
43 range-expanding populations have been demonstrated to rapidly adapt to novel environments in a
44 growing body of empirical studies (reviewed in Colautti and Lau 2015, Chuang and Peterson
45 2016), challenging the fundamental assumption of ENMs that niches are conserved in space and
46 time (Pearman et al. 2008). Newly developed mechanistic and hybrid species distribution models

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

53

54 Niche evolution has been studied extensively in invasive species, with studies comparing the
55 climate conditions occupied by populations in the native and invaded range. While there is
56 strong evidence that invading populations can rapidly evolve to reestablish adaptive clines along
57 environmental gradients similar to those in their native range (e.g., Boheemen et al. 2019),
58 whether species' ultimate niche limits are generally conserved during invasion (Petitpierre et al.
59 2012, Liu et al. 2020) or commonly shift (Early and Sax 2014, Atwater et al. 2018) is highly
60 debated. Niche stasis (*sensu* Pearman et al. 2008) is defined as the lack of change in either the
61 fundamental niche (the climate where a species can grow in the absence of biotic constraints and
62 geographic barriers) or realized niche (the actual climate conditions where a species is observed,
63 which is captured by ENMs). Niches may shift in the invaded range when not all areas with
64 similar climates are occupied (yet) due to dispersal limitation. Niche expansion occurs when
65 biotic interactions or dispersal barriers constraining the realized niche in the native range are
66 lifted in the new range, or when the fundamental niche itself evolves (Alexander and Edwards
67 2010). Examples of evolutionary changes that have been linked to climate niche expansion in
68 invasive populations include plant phenology responses to temperature or photoperiod (Dlugosch

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

71

72 Much less attention in the empirical literature has been paid to niche evolution during
73 contemporary native range shifts induced by climate change. Instead, species' responses to
74 global warming are commonly viewed as a “move, adapt, or die” conundrum, where populations
75 need to track suitable climates to higher latitudes and altitudes, or adapt *in situ*, or else they will
76 lag behind the pace of climate change and go extinct (Aitken et al. 2008, Corlett and Westcott
77 2013). However, poleward-spreading populations face a variety of novel abiotic (as well as
78 biotic) conditions, even if range expansion is initiated by climate change (Spence and Tingley
79 2020). For example, photoperiod and temperature seasonality increase non-linearly with latitude,
80 and plants experience a reduction in photosynthetically active radiation and light quality towards
81 the poles (Taulavuori et al. 2010, Saikkonen et al. 2012). These novel combinations of
82 temperature and photoperiod cues at higher latitudes require a plastic or evolutionary response
83 (Visser 2008). Thus, whether climate-mediated range shifts will involve simultaneous niche
84 evolution is now acknowledged as an important open question (Lee-Yaw et al. 2019, Nadeau and
85 Urban 2019). Recent empirical work has demonstrated rapid evolutionary responses to novel
86 abiotic conditions during contemporary native range shifts, including increased thermal niche
87 breadth in damselflies (Lancaster et al. 2015, Dudaniec et al. 2018) and earlier fall phenology in
88 plants (Lustenhauer et al. 2018). Palaeoecological studies of the Pleistocene glaciations have
89 shown that dispersal, plasticity, evolution and niche conservatism have all played a role in past
90 range shifts with climate change (Martínez-Meyer et al. 2004, Nogués-Bravo et al. 2018).

91 Historic constraints (or the lack of them) on range expansion may inform how evolution will
92 affect recent range shifts with climate change (Diamond 2018).
93
94 Comparing native range shifts and invasions provides valuable insights into the drivers of niche
95 evolution during range expansion in both native and exotic ranges. Quantifying rapid adaptation
96 to novel climates during invasions can inform predictions about the degree of evolutionary
97 change that may be expected during native range expansions on similar time scales (Moran and
98 Alexander 2014). Similarly, the likelihood of niche shifts in the invaded range depends on
99 whether the native range is limited by biotic interactions or fundamental evolutionary constraints
100 such as genetic correlations between traits (Alexander and Edwards 2010). Yet there are also
101 differences between native and exotic range expansions in key processes driving evolutionary
102 change, most notably the level of gene flow. Disconnection from the historic native range could
103 lead to increased niche evolution in invading populations (Jakob et al. 2010), unless genetic
104 diversity and population sizes are too low (Hoffmann and Sgrò 2011). However, genetic
105 bottlenecks have little impact in invasions founded by multiple introductions (Dlugosch and
106 Parker 2008b, Smith et al. 2020). In the native range, the impact of ongoing gene flow will
107 depend on whether it has a maladaptive swamping effect or increases evolutionary potential, an
108 issue which is highly debated (Kottler et al. 2021). Theory suggests that adaptation during range
109 expansion under gene flow is governed by the balance between selection and genetic drift on the
110 one hand, and the steepness of the environmental gradient on the other hand (Polechová and
111 Barton 2015). Overall, authors have hypothesized that niche shifts are more common or rapid in
112 exotic than in native range expansions (Pearman et al. 2008, Wiens et al. 2019), but the empirical
113 data required to test this idea are largely absent.

114 In this study, we examine climate niche evolution during both native and exotic range expansion
115 by taking advantage of a species currently involved in both types of population spread. *Dittrichia*
116 *graveolens* (L.) Greuter is an annual plant in the Asteraceae with a native distribution around the
117 Mediterranean Basin (Brullo and De Marco 2000). The species has greatly expanded its native
118 range northward since the mid-20th century, coincident with rapid evolution of earlier flowering
119 time at the leading edge in response to shorter growing seasons (Lustenhouwer et al. 2018). *D.*
120 *graveolens* has a ruderal life history and produces large numbers of wind-dispersed seeds,
121 facilitating spread along roads where biotic interactions with other plant species play a minor
122 role in its ecological success. The species has invaded worldwide in most other regions with a
123 Mediterranean climate - first Australia (1860s; Parsons and Cuthbertson 2001) and South Africa
124 (GBIF.org 2020), then California (1980s; Preston 1997), and most recently Chile (Santilli et al.
125 2021). In Australia and California, *D. graveolens* is considered a noxious weed of high
126 management concern due to a combination of rapid spread and toxicity to livestock, impacts on
127 native plant communities, and human skin allergies (Parsons and Cuthbertson 2001, Brownsey et
128 al. 2013b, USDA 2013).

129

130 We ask: (a) Did *D. graveolens* simply track climate change during the native range expansion, or
131 was range expansion promoted by climate niche evolution? (b) Is there evidence of niche shifts
132 in the invaded ranges? (c) How does taking into account climate niche evolution during the
133 native range expansion change invasion predictions for California and Australia? To answer
134 these questions, we applied the COUE scheme of niche centroid shift, overlap, unfilling and
135 expansion (Guisan et al. 2014) to *D. graveolens*' native range expansion with climate change
136 (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

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

174

175 *Defining the historic native range limit*

176 *D. graveolens*' historic native distribution is centered around the Mediterranean Basin, extending
177 eastward to the Middle East and NW-India, and northward into central France (Tutin et al. 1976,
178 Brullo and De Marco 2000). The first records of a large-scale northward range expansion of *D.*
179 *graveolens* appear for the 1950s in northern France, initially associated with salt mines and
180 followed by abundant spread along roads (Wagenitz 1966, Ciardo and Delarze 2005, Parent
181 2011). We chose 1901-1930 as the pre-expansion time window for our study, which matches the
182 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 $\beta=0.5$. 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

275 potential risk of invasion in California and Australia, we applied a Minimum Presence Threshold
276 (the lowest habitat suitability at which *D. graveolens* is already present in the invaded range).

277 We then compared projections generated by the Past and Present model for each invaded range.

278

279 **Results**

280 Over the course of less than a century, *D. graveolens* has shifted its native range limit northward
281 by nearly 7 degrees latitude. During this range expansion, the climate niche expanded by 5% to
282 include more temperate environments with lower diurnal range and precipitation seasonality
283 (bio2, bio15), increased precipitation in the driest and warmest quarters (bio17, bio18), and
284 increased temperature seasonality (bio4) and fall frost (Fig. 1a,b). Niche overlap (Schoener's $D =$
285 0.71) of the historic and expanded native niche was significantly lower than expected by chance
286 (niche equivalency test; Fig. 1c, Table 2), indicating a niche shift during range expansion.

287 Nonetheless, the two niches were more similar to each other than to randomly selected niches in
288 the study area (niche similarity test; Fig. 1d, Table 2). Niche expansion was not driven by
289 climate change between the past and present period, which happened in a different direction in
290 environmental space (reduced frost and temperature seasonality; Fig. 1a).

291

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

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

304

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

318

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

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

328

329 **Discussion**

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

340

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

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

357

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

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

416

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

428

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435

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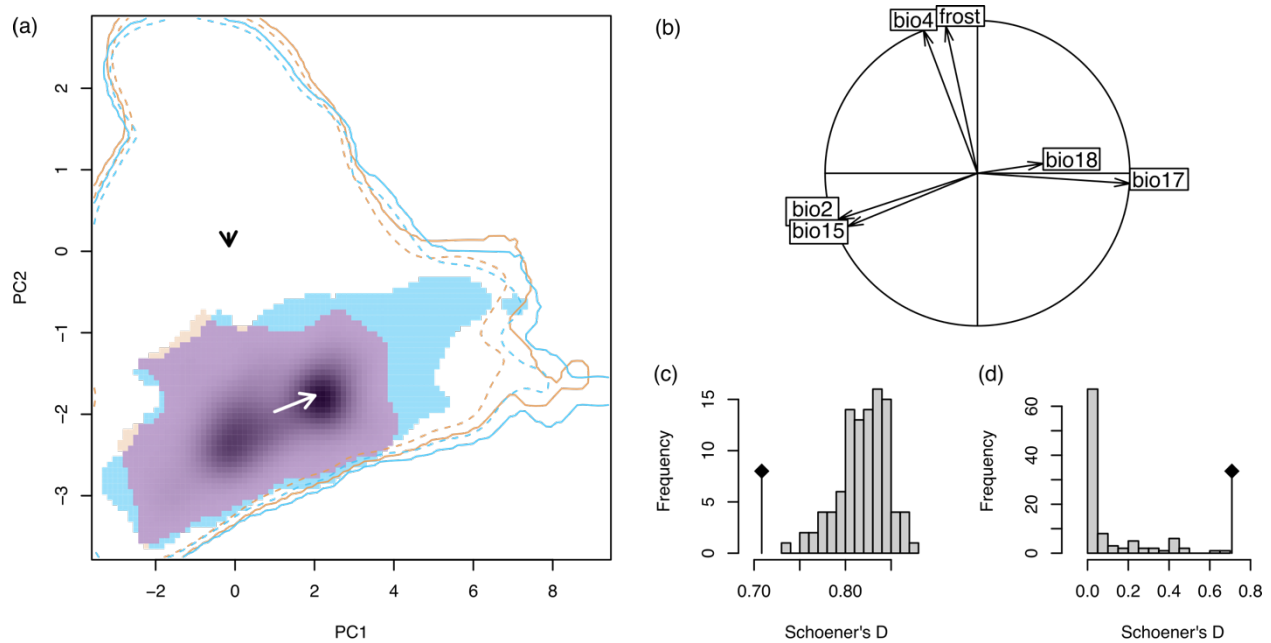
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- 640

641 **Figures**

642



643

644 **Figure 1** Niche shift during native range expansion, comparing the past (1901-1930) and present

645 (1990-2019) datasets; (a) past and present niche in environmental space, with colors indicating

646 niche stability (purple), unfilling (orange) and expansion (blue), and the white arrow showing the

647 niche centroid shift. Dark shading shows the density of occurrences in the historic range. Lines

648 represent the climate of the Eurasian Holarctic in the past (orange) and present (blue), using

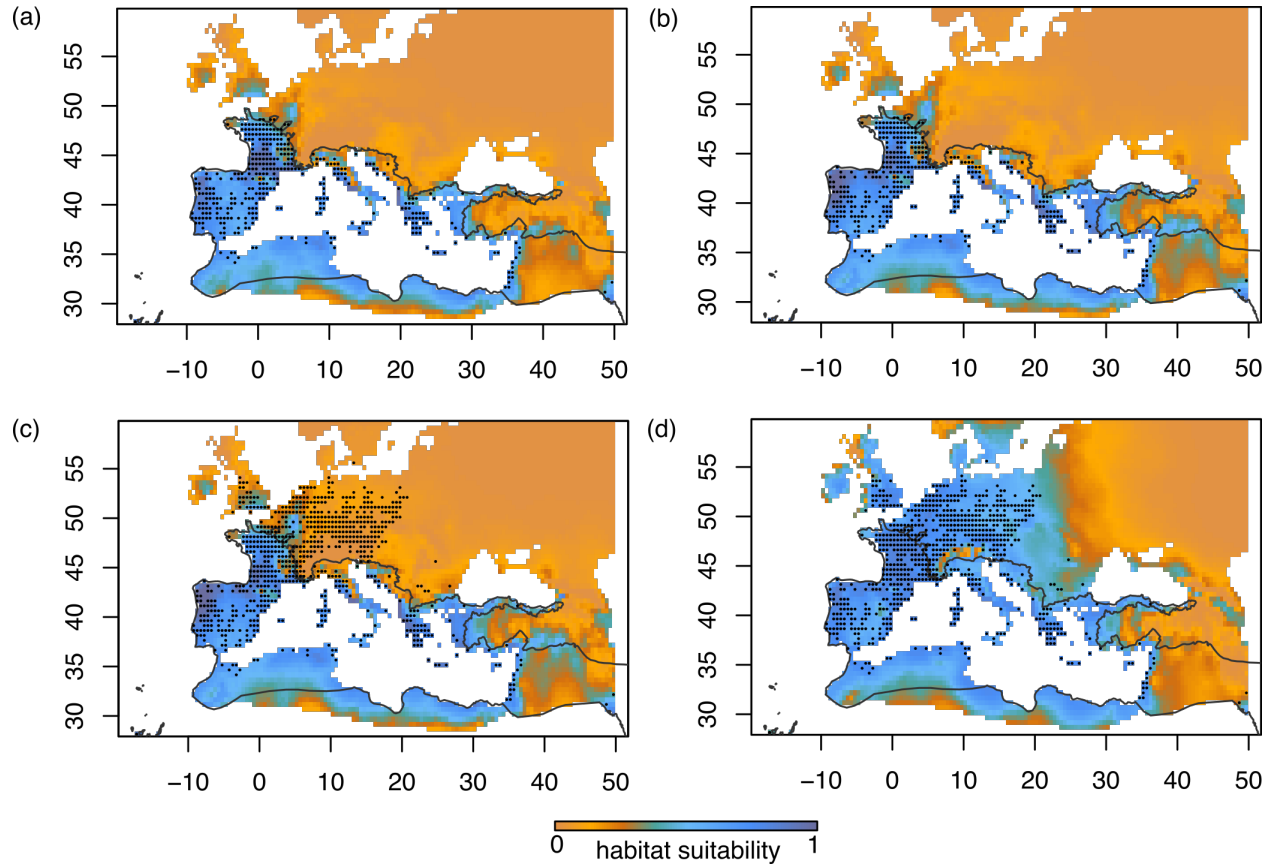
649 100% (solid) and 90% (dashed) of available climates. The black arrow indicates the climate

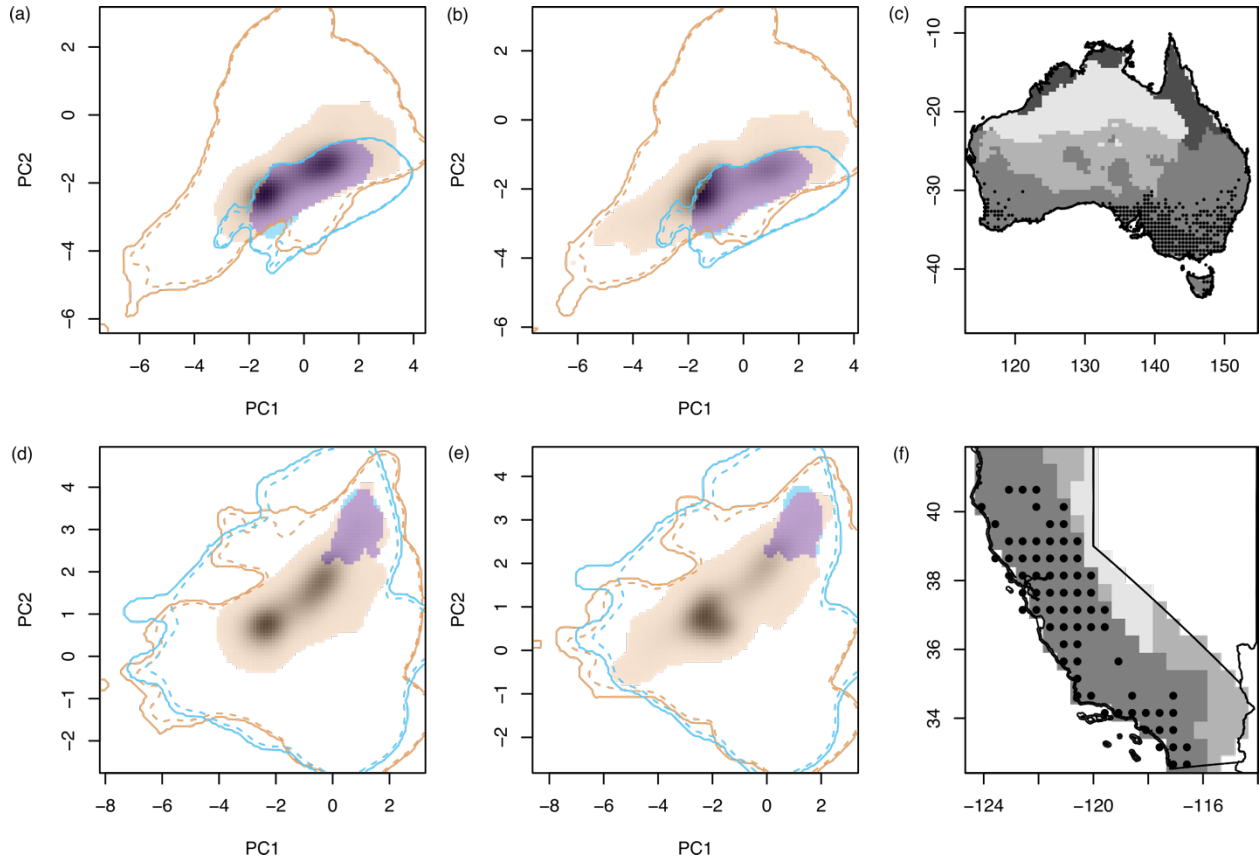
650 centroid shift between past and present. (b) principal component analysis of the entire

651 environmental space, with axes explaining 41.6% (x) and 29.0% (y) of variation. Arrows show

652 environmental predictors as defined in Table 1. (c, d) niche equivalency and niche similarity test,

653 with histograms showing null distributions and diamonds marking observed niche overlap.





663

664 **Figure 3** Niche shift during invasion in Australia (a,b) and California (d,e), using the past native

665 (a,d) and present native (b,e) niche and climate as a reference. Colors indicate niche stability,

666 unfilling and expansion as in Fig. 1, with lines representing the climate of the native (orange) and

667 exotic (blue) study area. Shading shows the density of occurrences from the historic (a,d) and

668 expanded (b,e) native range in environmental space. Panels c and f show areas at risk of invasion

669 as projected by the Past and Present Model, with cells shaded from dark to light as follows: cell

670 included in the Past Model only, in both models, in the Present Model only, or in neither model.

671 Points indicate observation records for *D. graveolens* in Australia (c) and California (f).

672

673 **Tables**

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

675 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

676 **Table 2** Niche shift metrics following the COUE framework, calculated using the intersection of

677 the 90th percentile of environmental conditions in each range. Niche equivalency and similarity

678 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

679

680 **Table 3** Maxent model performance for projections of the Past Model in both time periods, and

681 the projection of the Present Model in the present. All presence and background points were

682 allocated randomly to training and test datasets using 5 k-folds for cross-validation (table shows

683 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

684