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Mechanistic species distribution modeling reveals a niche shift during invasion

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Abstract. Niche shifts of nonnative plants can occur when they colonize novel climatic conditions. However, the mechanistic basis for niche shifts during invasion is poorly understood and has rarely been captured within species distribution models. We quantified the consequence of between-population variation in phenology for invasion of common ragweed (*Ambrosia artemisiifolia* L.) across Europe. Ragweed is of serious concern because of its harmful effects as a crop weed and because of its impact on public health as a major aeroallergen. We developed a forward mechanistic species distribution model based on responses of ragweed development rates to temperature and photoperiod. The model was parameterized and validated from the literature and by reanalyzing data from a reciprocal common garden experiment in which native and invasive populations were grown within and beyond the current invaded range. It could therefore accommodate between-population variation in the physiological requirements for flowering, and predict the potentially invaded ranges of individual populations. Northern-origin populations that were established outside the generally accepted climate envelope of the species had lower thermal requirements for bud development, suggesting local adaptation of phenology had occurred during the invasion. The model predicts that this will extend the potentially invaded range northward and increase the average suitability across Europe by 90% in the current climate and 20% in the future climate. Therefore, trait variation observed at the population scale can trigger a climatic niche shift at the biogeographic scale. For ragweed, earlier flowering phenology in established northern populations could allow the species to spread beyond its current invasive range, substantially increasing its risk to agriculture and public health. Mechanistic species distribution models offer the possibility to represent niche shifts by varying the traits and niche responses of individual populations. Ignoring such effects could substantially underestimate the extent and impact of invasions.

Key words: biological invasion; climate change; common ragweed; ecological niche model; niche conservatism; process-based model; rapid evolution.

INTRODUCTION

Biological invasions are a major component of anthropogenic global change, causing widespread ecological and socioeconomic harm (Vilà et al. 2011). Understanding the mechanisms governing spread into new territory following deliberate or accidental release is central to predicting and managing their negative impacts. Among these, evolutionary change may contribute to the success of many nonnative species (Parker et al. 2003, Sax et al. 2007, Prentis et al. 2008). Biological invasions are often associated with strong founder effects, multiple introductions, hybridization and selection in novel environments, which can all promote rapid evolutionary change (Bossdorf et al. 2005, Dlugosch

and Parker 2008). This can lead to phenotypic differentiation in demographically important traits between native and introduced ranges, as well as among invasive populations (Colautti et al. 2009, Li et al. 2015). However, the effect of such changes on the range expansion and impacts of nonnative species is poorly understood especially regarding the extent to which local adaptation has extended the actual or potential invaded range of nonnative species (Kolbe et al. 2010).

There is also emerging evidence for niche shifts during invasion from studies at biogeographic scales (Broennimann et al. 2007, Pearman et al. 2008). These assess whether climatic associations of a species differ between regions, such as native and nonnative continents, from which a change in the realized niche is inferred (Broennimann et al. 2007, Early and Sax 2014). Importantly, this suggests that species distribution models trained on the native range will be poorly transferable in space or time, and may under-predict the potentially invaded distribution and climate-driven range shifts (Early and Sax

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2014, Parravicini et al. 2015). Even though some have suggested that niche shifts during plant invasions are rare (Petitpierre et al. 2012) it is possible that they may take a long time to manifest. Initial invasion of habitats analogous to the native conditions may be followed by a period of adaptation to novel environments that expand the niche and invaded range (Broennimann et al. 2007, Prentis et al. 2008). This argues for a greater integration of studies on evolutionary change during invasion at population and biogeographic scales.

Forward mechanistic species distribution models (Dormann et al. 2012) offer a potentially useful tool for such integration. Mechanistic (or process-based) distribution models attempt to formulate the niche in terms of the causal effects of climate and other environmental factors on functional traits that affect demography and therefore distribution (Kearney and Porter 2009, Evans et al. 2016). “Forward” models are developed by empirical parameterization of the underlying process rather than by calibration against distribution data (Chapman et al. 2014, Evans et al. 2016). For example, one might determine experimentally the effect of temperature on development of a trait whose values determine one or more demographic rates in the model. Because this avoids problems associated with fitting to distributions that are not equilibrated to the environment, it is potentially very advantageous for distribution modeling of invasive species, as well as species that are already shifting distributions due to climate change (Dormann et al. 2012). Further, if populations of a species differ in trait responses to temperature, potentially through local adaptation, a forward model can quantify any niche shift or distributional change resulting from this differentiation (Kearney et al. 2009, Valladares et al. 2014). However, mechanistic distribution models have rarely been applied to study niche shifts arising from observed trait differentiation among populations of invasive species (Kolbe et al. 2010).

In this study, our objective was to demonstrate how a forward-mechanistic species distribution model can be used to simulate a potential niche shift of common ragweed (*Ambrosia artemisiifolia* L.) during its invasion of Europe. Ragweed is a globally invasive, noxious, annual weed, native to North America and spreading in human-modified habitat in Europe and other temperate regions (Fig. 1; Essl et al. 2015, Chapman et al. 2016). It severely impacts public health via highly allergenic airborne pollen (Prank et al. 2013, Smith et al. 2013, Hamaoui-Laguel et al. 2015) and is an important agricultural weed (Essl et al. 2015), so predicting its potential distribution is important for risk assessment and management planning. Rather than inferring a niche shift from distributional changes, we instead directly modeled between-population variation in phenology, a trait that plays a key role in defining the niche and distribution of many species (Chuine 2010). To parameterize a phenology model for individual native and invasive populations, we reanalyzed data from a common garden

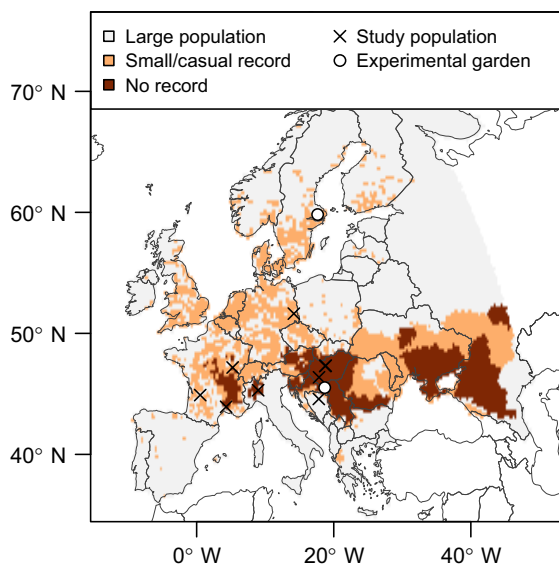


FIG. 1. Nonnative distribution of common ragweed (*Ambrosia artemisiifolia*) in the modeled region of Europe (records from 1991–2010 on a 0.25° grid). Based on pollen monitoring data (Prank et al. 2013, Smith et al. 2013, Hamaoui-Laguel et al. 2015) the occurrences were classified as either invasive and damaging populations, or small or casual populations due to human introduction rather than climatic suitability (Appendix S1). Symbols locate the experimental populations and gardens (Scalone et al. 2016) used to parameterize our models.

phenology experiment carried out within and beyond the invaded range (Scalone et al. 2016). We then used this information in a phenology-based mechanistic distribution model (Chapman et al. 2014) for each ragweed population, making potential distribution projections in the current and future projected climates. We interpreted between-population variation in potential distributions, associated with their phenological differences, as representing a potential niche shift.

METHODS

Study species

Ragweed has been accidentally imported and released into Europe on numerous occasions, for example, as a contaminant of crop and bird seed (Chapman et al. 2016). As a result, casual populations of the species have been recorded throughout much of Europe. However the species has only been able to establish large and invasive populations in continental regions (Fig. 1) where climatic conditions are similar to those in the native distribution (Cunze et al. 2013, Essl et al. 2015, Chapman et al. 2016).

Species distribution models indicate that cool temperatures limit ragweed's northern invasive range, causing concern that climate change will drive major expansion of ragweed's distribution and impacts (Cunze et al. 2013,

Chapman et al. 2014, Storkey et al. 2014, Hamaoui-Laguel et al. 2015). However, it has been suggested that ragweed's photoperiod response may limit northward expansion in a warmer climate (Chapman et al. 2014, Scalone et al. 2016), since it is a quantitative short day plant requiring long nights to flower and set seed before lethal winter frosts (Essl et al. 2015). Changes in ragweed's phenological responses through selection or other mechanisms could overcome this constraint, representing a shift in the fundamental and realized niches. Ragweed seemingly has a high adaptive potential due to repeated introductions, high outcrossing and high genetic diversity (Genton et al. 2005, Friedman and Barrett 2008). Indeed, compared to native populations, invasive ragweed populations exhibit faster juvenile growth, more frost tolerant seeds and larger size (Hodgins and Rieseberg 2011, Leiblein-Wild et al. 2013). Moreover, latitudinal clines in flowering phenology are known within the native and invasive distributions and most probably represent local adaptation (Hodgins and Rieseberg 2011, Li et al. 2015, Scalone et al. 2016).

Phenology model

Our generic plant phenology model uses the concept of physiological time to simulate plant development in chronological time (Chuine 2000, Trudgill et al. 2005). For a given chronological hour, the physiological hour experienced by the plant is the proportion of the development that would have occurred at optimal growing conditions (here, temperature and photoperiod) that the plant achieves. This is commonly referred to as forcing or chilling. Assuming development proceeds at a constant rate in physiological time, a fixed amount of physiological time must pass for completion of each phenological stage. This allows events such as germination or flowering to be modeled as the chronological time at which sufficient physiological time has accumulated (Chuine 2000).

For ragweed, the model represents the sequential phenology of seed dormancy breaking, germination, seedling emergence, bud appearance, female (pistillate) flower appearance and development of mature seed (Deen et al. 2001, Chapman et al. 2014). As with many short-day annuals, temperature is the primary driver of modeled phenological development, though appearance of female flowers is also negatively affected by long photoperiods (Deen et al. 1998). Each phenological event in the model requires a forcing function and a critical threshold of cumulative forcing to trigger the event (Table 1 and Appendix S2 for full details). The model is very similar to our earlier model (Chapman et al. 2014) with the principal differences being the inclusion of a mechanistic model for seed dormancy breaking, population-specific critical thresholds for bud and female flower development, and the temperature data used in forcing phenology (see below).

Between-population variation in phenology

Based on newly published common garden experiment data (Scalone et al. 2016), we were able to represent between-population variation in the thresholds for bud and female flower development in the model. To quantify this, we reanalyzed data in which ragweed plants were grown in Sweden (59.8° N 17.6° W, beyond the northern limit of the invaded distribution, 20 individuals per population) and Croatia (45.5° N 18.7° W, core of the invaded distribution, 10 individuals per population; see Fig. 1; Scalone et al. 2016). Plants came from 12 populations, three North American native (38.0–45.1° N) and nine European nonnative (43.9–51.6° N; Fig. 1). Emerging seedlings were grown indoors and then transplanted outdoors where individual dates of female (pistillate) flower appearance were recorded. In the Swedish garden, bud appearance was also recorded.

TABLE 1. Summary of the ragweed phenology model (see Appendix S2 for full details).

Developmental event	Hourly forcing function	Cumulative forcing required (h)
Seed dormancy breaking	$f(T) = \frac{a + bT_{\text{opt}} + cT_{\text{opt}}^2}{a + bT + cT^2} \dagger$	1030.6
Seed germination	$g(T) = \left(\frac{T - T_{\text{min}}}{T_{\text{opt}} - T_{\text{min}}} \left(\frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}} \right)^{\frac{T_{\text{max}} - T_{\text{opt}}}{T_{\text{opt}} - T_{\text{min}}}} \right)^c \ddagger$	82.0
Seedling emergence	$g(T)$	24
Bud appearance	$g(T)$	varies by population
Female flower appearance	$g(T)h(L)$	varies by population
Seed maturation	$h(L) = \min(1, \exp[(L - L_0)\ln(1 - \alpha)]) \S$ $g(T)$	456

Notes: The model represents six sequential developmental events, forced by hourly temperature (T [°C]) and/or photoperiod (L [h]). Progression through each stage requires the accumulation of a certain threshold of forcing over the hourly time steps of the model. Based on experimental data, the model includes between-population variation in the cumulative forcing required for development from emergence to flowering.

\dagger $a = 1921.7$, $b = -331.0$, $c = 30.75$, $T_{\text{opt}} = -b/2c = 5.4^\circ\text{C}$.

\ddagger $T_{\text{min}} = 3.652^\circ\text{C}$, $T_{\text{opt}} = 34.01^\circ\text{C}$, $T_{\text{max}} = 40.00^\circ\text{C}$, $c = 1.552$.

\S $L_0 = 14.0$ h, $\alpha = 0.396$.

Scalone et al. (2016) analyzed the dates of various phenological events of these populations in each experimental garden, finding clear latitudinal clines. Here, we used a subset of their data to parameterize our phenology model for each population by estimating the median thermal and photothermal requirements for bud and flower appearance. We first estimated the median dates of bud and flower appearance of each population in each garden using a right-censored Weibull model (Odell et al. 1992; also see Appendix S3). Estimates were only made where <50% of plants were censored (did not bud or flower during the experiment), which unfortunately excluded two of the three native populations from our analysis. For the Swedish garden, the median thermal hours from emergence to bud appearance and photothermal hours from bud appearance to female flower appearance were then characterized for each population using the functions in Table 1. This parameterizes the phenology model for each population. The model was then validated by predicting the flowering dates for each population in Croatia reported by Scalone et al. (2016).

To estimate model phenology, daily outdoor minimum and maximum temperatures for the gardens were extracted from the E-OBS v11.0 database, which is a gridded product derived by interpolating weather stations (Haylock et al. 2008). These were downscaled to an hourly resolution using the *chillR* R package (Luedeling 2015). This employs an idealized temperature curve following a sine curve for daytime warming and logarithmic decay for nighttime cooling. Daily photoperiods were estimated using the *geosphere* R package (Hijmans et al. 2015).

Forward mechanistic distribution model

To estimate the extent to which the observed between-population variation in phenology could trigger a niche shift in Europe, we used the phenology model to predict the climatic suitability of each individual population. As a measure of suitability we calculated the proportion of years in which thermal and photoperiodic conditions were adequate for median seed maturity to occur before autumn frost (Chapman et al. 2014). Phenology was simulated independently in each 0.25° grid cell of Europe, using gridded daily temperatures from the E-OBS v11.0 data set for each year between 1991 and 2010 (Haylock et al. 2008). This 20-yr period corresponds to our database of ragweed occurrence records (Fig. 1; Chapman et al. 2014). In each grid cell, daily temperatures downscaled to an hourly resolution as above. This could not be done in Arctic regions during times with 24 h of either daylight or darkness, so in these cases, we used linear interpolation between minimum and maximum temperatures with 12-h periodicity. Accumulation of forcing began on the first day of the year. Termination of the growing season occurred when temperatures fell to a lethal -5°C (Dahl et al. 1999, Leiblein-Wild et al. 2013). This represents an important deviation from our

previous model, which was based on long-term average daily temperatures falling to -5°C (Chapman et al. 2014). With the actual daily temperatures used here, a lethal frost event could occur much earlier than indicated by long-term average temperatures. A sensitivity analysis explored the effects of model initiation date and lethal frost temperature on the model predictions.

The model predicts the ability of a typical individual (having median physiological time requirement) to set seed in each year, providing a measure of climatic suitability. However, translating this climatic suitability into a likelihood of establishment is not trivial. The typical individual probably does not need to set seed in every single year to sustain long-term population growth because ragweed has a persistent seedbank and there is a large amount of within-population variability in phenology. Since the critical proportion of years with seed set needed for population persistence is not known, we assessed the accuracy of the predictions using a threshold-independent measure of discriminatory performance, the Area Under the receiver operating characteristic Curve (AUC). Specifically, AUC was calculated on predicted suitability in the grid cells in which large populations are known to have established vs. the grid cells where ragweed has been introduced but only small or casual populations have been able to establish (see Fig. 1). This avoids problems with “absence” of an invasive species in climatically suitable areas because of limited propagule pressure or under-recording.

Future range projection

To investigate potential climate-driven changes in invasion, we ran the mechanistic distribution model for a future climate scenario. This required climate model simulation of daily minimum and maximum temperatures at similar spatial resolution to the current-day data. From the PRUDENCE project we obtained simulated European daily air temperatures from a run of the HIRHAM regional climate model on a rotated 0.22 degree grid (Christensen and Christensen 2007). We ran the distribution model for these data, and then projected the output onto the 0.25° regular grid used for the current climate.

These data were only available for scenario A2 of the Special Report on Emissions Scenarios (SRES) in the 2080s (2076–2095). SRES A2 represents a world of increasing population growth, economic development and regionalization and is at the upper end of the SRES emissions scenarios (Nakicenovic and Swart 2000). Although this is a rather distant time period and not among the most recent set of emissions scenarios, the availability of high resolution daily data favored the use of SRES A2 for the 2080s. Furthermore, our objective was to illustrate how between-population variation in phenology can affect potential responses to climate change rather than provide specific predictions of range shifts, so the exact choice of scenario was not critical.

RESULTS

Parameterization and validation of the phenology model

The phenology model was parameterized for each of the 10 included populations by converting estimated budding and flowering times in Sweden from Scalone et al. (2016) into total amounts of elapsed physiological time (Fig. 2a; Appendix S3: Table S1). Estimates of the median thermal hours from seedling emergence to bud appearance for each population were negatively correlated to their latitude of origin ($r = -0.950$, $df = 10$, $P < 0.001$; Fig. 2a). By contrast, the photothermal times from bud to flower appearance in Sweden were similar across populations and not significantly correlated to latitude ($r = -0.396$, $df = 8$, $P = 0.258$; Fig. 2a). Interestingly, the mean physiological times for bud and flower appearance in the experiment (1,032 and 302 physiological hours, respectively) exceeded those reported in the native range (276 and 108 h; Deen et al. 2001).

The model was validated by showing that physiological time requirements in Sweden predicted median flowering dates of the populations in Croatia with $R^2 = 0.906$, root mean squared error (RMSE) of 3.0 d and mean error (ME) of 2.0 d (Fig. 2b). This indicates an accurate but slightly late-biased estimation of flowering dates in Croatia, which we considered acceptable for using the model to predict phenology.

Mechanistic species distribution model

Using the phenology model parameterized with each population's physiological time requirements shown in Fig. 2a, we predicted the proportion of years for which the median individual in each population sets seed before a lethal frost occurs (Appendix S4: Fig. S1). This provides a measure of climatic suitability for ragweed

invasion, with respect to temperature and photoperiod (but ignoring other potential limiting factors such as drought or availability of disturbed habitats). To visualize predictions from multiple populations on one map, we summed the number of populations where climatic suitability was $>50\%$ (Fig. 3a, b). This arbitrarily threshold was selected for visualization and does not necessarily represent a minimum suitability for occurrence. The maps suggest that phenological differentiation of the northernmost invasive population substantially increases the potentially invaded distribution. Northern-origin populations had higher mean climatic suitability across Europe (Fig. 3c, $r = 0.925$, $df = 8$, $P < 0.001$). Indeed the northernmost population had a mean suitability over the modelled region of 59%, compared to a mean of 31% for the other modeled populations.

To evaluate the potential adaptive significance of the observed phenological differentiation among invasive populations, we compared climatic suitability of each population in their European locations of origin (Fig. 3c). All populations had high suitability at their own origin location (successful seed set by the median individual in $\geq 85\%$ of years) and in origins from further south (not shown). However most populations had very low suitability at the location of the northernmost population, outside of the generally accepted climatic niche of the species (successful seed set in $\leq 15\%$ of years). The only exception to this was the northernmost population itself, which performed strongly in its home location.

Model prediction accuracy for the invasion of Europe (AUC between large invasive and small/casual records) was comparable and fairly high for all the populations originating south of 50° N but substantially lower for the northernmost population (Fig. 3d). Sensitivity analysis showed that these results were not qualitatively affected by the choice of model starting day or lethal frost temperature (Appendix S5).

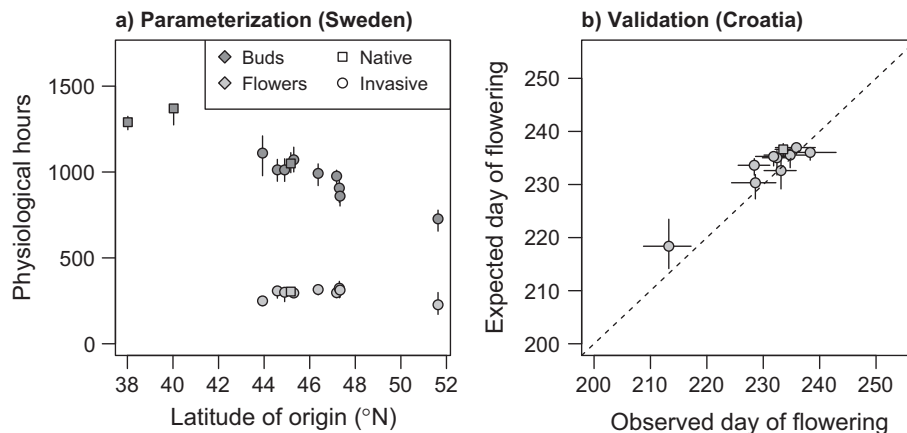


FIG. 2. (a) Parameterization of the phenology model for nine invasive and three native ragweed populations, quantified in a common garden in Sweden. This reveals latitudinal clines in the physiological times needed for development of buds (thermal hours) and flowers (photothermal hours), as the plot shows medians and 95% highest posterior density intervals estimated from the data of Scalone et al. (2016). (b) Model validation by predicting flowering dates in Croatia for the 10 populations flowering in Sweden. Two native populations did not flower in Sweden so could not be modeled.

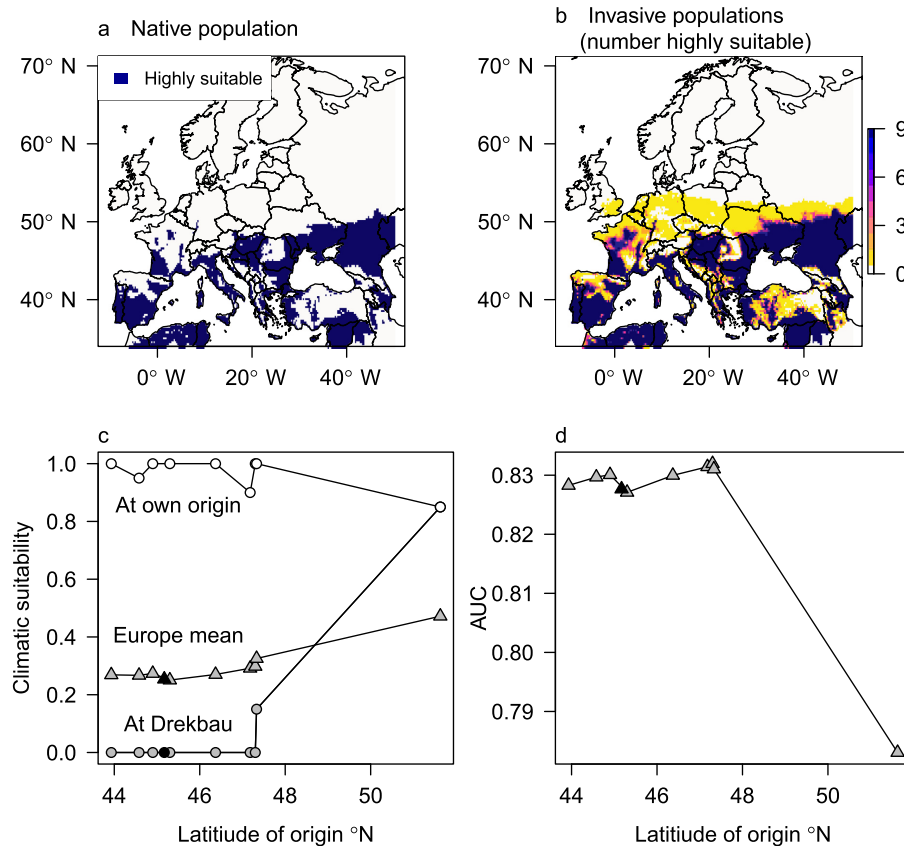


FIG. 3. Predicted potential ragweed invasion of Europe in the current climate (1991–2010). (a) Areas of high climatic suitability for invasion by the native population, with respect to thermal and photoperiodic constraints (median individual sets set in at least 50% of years). (b) The number of invasive populations meeting the same criteria. The single population substantially extending the potentially invaded region is the northernmost invasive one. (c) The relationship between latitude of origin and predicted climatic suitability for invasion across all of Europe (Europe mean), at their own origin location and the northernmost invasive population's origin (Drekbau, Germany). The latter two lines meet at the northernmost population origin. Black points represent the native population. (d) Model fit for each population, quantified as the Area Under the Curve (AUC) for heavily invaded grid cells vs. those where the species has been introduced but not become highly invasive.

Future climate change prediction

When the model was run with regional climate model outputs for the 2080s under SRES scenario A2, the predicted potential ranges of all ten populations increased in area because of substantial northward expansion (Fig. 4). Because of its earlier flowering, the northernmost invasive population was predicted to be capable of reproduction in most years as far north as central UK and Ireland, Denmark, southern Sweden and most of the southern Baltic coast. For this population, the mean suitability across Europe was 75%, compared to a mean of 62% for the other populations.

DISCUSSION

Species distribution models have become central for understanding species–environment interactions and projecting distributional changes in climate-change ecology and invasion biology (Elith et al. 2010, Chapman

and Purse 2011, Dormann et al. 2012, Evans et al. 2016). However, their success relies upon an assumption of niche conservatism in space and time (Broennimann et al. 2007, Pearman et al. 2008, Early and Sax 2014, Valladares et al. 2014, Parravicini et al. 2015). Changes in realized niches during invasion events have been observed from biogeographic studies (Broennimann et al. 2007, Early and Sax 2014) but their mechanistic basis remains largely unknown. To our knowledge only one other study has modeled niche shifts and distributional changes arising from observed between-population differentiation in functional traits of an invasive species (Kolbe et al. 2010).

Our reanalysis of published experimental data (Scalone et al. 2016) showed that between-population divergence in phenology was largely driven by a trend for lower thermal time requirements to produce flower buds in populations originating from higher latitudes. Photo-thermal time requirements for subsequent female flower development were similar among populations

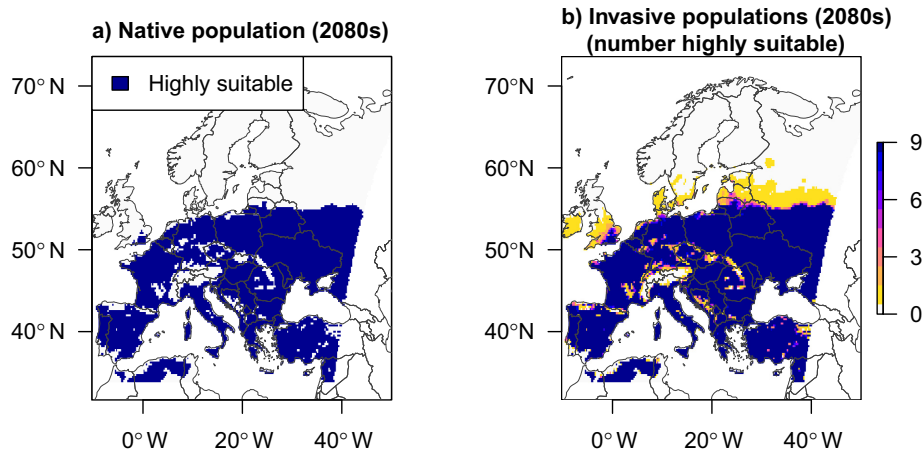


FIG. 4. Effect of climate change on the potentially invaded ranges of the native and nine invasive ragweed populations, equivalently to Fig. 3a, b. Distribution model projections were made for the 2080s (2076–2095) forced by a regional climate model's predictions for the SRES A2 emissions scenario. [Color figure can be viewed at wileyonlinelibrary.com]

and not correlated to latitude. This is strongly suggestive of local adaptation during the invasion, caused by selection to shorter growing seasons in northern Europe (Scalone et al. 2016). This explanation is supported by the phenology model indicating a selective advantage of the northernmost population over the other study populations in its home location in Germany, where native and southern invasive populations reproduced poorly. Furthermore it is consistent with a general expectation that phenological constraints on plant development can constrain species distributions and produce strong selective pressure (Chuine 2010, Colautti and Barrett 2013, Chapman et al. 2014).

Using these validated physiological times to parameterize our mechanistic distribution model, we showed that between-population differentiation in phenology has triggered a niche shift likely to substantially increase ragweed's potentially invaded range in both current and future climates. For the northernmost invasive population in particular, we predict a high suitability for extensive colonization across northwestern Europe, where cooler summers and shorter growing seasons have limited ragweed establishment and spread until now (Cunze et al. 2013, Chapman et al. 2014, 2016, Storkey et al. 2014). Throughout the past century, ragweed seeds have been repeatedly introduced accidentally to northern Europe, but have largely failed to establish and invade (Essl et al. 2015). The implication from our model is that early flowering in the northernmost established population has extended ragweed's niche, but it has yet to spread to its full extent in Europe. Therefore, ragweed's invasion may currently be in a second "lag phase" (Crooks 2005), in which the core niche space in central Europe has largely been filled, and where selection on traits including phenology in peripheral established populations will allow further northward spread. If so, then eradicating or restricting dispersal from isolated established populations

in northern Europe must be a management priority to avoid ragweed's major impacts on agriculture and public health.

We suggest that forward mechanistic (or process-based) distribution models (Dormann et al. 2012, Evans et al. 2016) offer several advantages for the assessment of niche shifts in nonnative species. First, clear hypotheses about the species' distribution are formulated in the model and tested against independent distribution data (Kearney et al. 2009). Here, we hypothesized that ragweed's invasive distribution is limited by thermal and photoperiodic phenological constraints (Chapman et al. 2014) and this was supported by the accuracy of our independent predictions of ragweed's current invasive distribution for populations from the native range and invaded range core. Second, unlike fitted distribution models (mechanistic or correlative), forward models do not require the distribution to be in equilibrium with the environment (Elith et al. 2010). This is critically important for nonnative species that do not yet fill all available niche space, as was exemplified by the predicted potential distribution of the northernmost population exceeding the current invasive distribution. Third, mechanistic models provide a clear link between changes to functional traits of the species and their consequences for niche and distributional shifts (Kolbe et al. 2010). Here, we showed that the early flowering of the northernmost established population triggers a niche shift toward cooler climates.

The mechanistic distribution model presented here is a development of our earlier model, which predicted a larger potential invasive distribution in Europe (Chapman et al. 2014). The major reason for this was that the physiological times for bud and flower appearance observed in the common garden experiment are greater than published estimates in the native range (Deen et al. 2001) and used in the former model. Because our current

parameterization accurately predicted flowering times and the distribution of invasive populations in Europe we suggest it is more reliable. We also suggest that the model presented here is simple and generic enough that it could be modified for wider application to other species, especially other problematic annual weeds (e.g., *Xanthium strumarium*, *Centaurea solstitialis*, *Amaranthus retroflexus*, *Chenopodium album*). However, it is important to understand what its outputs mean. The parameterization of phenology was based upon the median individual in each population. Therefore, the modeled climatic suitability measure is the proportion of years in which the median individual successfully sets seed, given the local thermal and photoperiodic conditions. This yielded a strong discrimination ability for the observed invasive ragweed distribution, but could no doubt be improved by incorporation of other limiting factors such as drought into the physiological time equations (Cunze et al. 2013, Storkey et al. 2014, Essl et al. 2015, Chapman et al. 2016). Furthermore, drought and other factors can limit the niche through their effects on mortality or reproductive success as well as through phenology, arguing for an integration of phenology and demography in the future development of mechanistic species distribution models (Evans et al. 2016). We did not bring drought into the current model since we wished to preserve its simplicity and forward predictive nature and because our primary interest is range expansion into northern Europe, where drought is not limiting.

A further limitation of the current model, and mechanistic species distribution models generally, is that it relies on empirical parameterization for individual populations. This is laborious and may not sample the full range of phenotypes across the species' range (Evans et al. 2016). To move toward a more predictive framework it would be desirable to find general ways to predict the effect of phenology on fitness (Colautti and Barrett 2013). For ragweed, we suggest that developing the current model to include seed production would be a useful next step. One may hypothesize that flowering too early means seed production will be limited allometrically by insufficient resource acquisition, while flowering too late means seed maturation will be prevented by frost. A model of this trade-off could allow identification of the fitness-maximizing phenological phenotype in each location. In combination with knowledge of minimum resource requirements for reproduction, such an approach could quantify theoretical limits on niche shifting and simulate eco-evolutionary responses to novel climates and future climate change (Kearney et al. 2009). Since niche shifts of invasive species may be relatively common (Early and Sax 2014) there are clear benefits in improving our understanding of these processes and in making better predictions of niche shifts during invasion.

Here, we provide one of the first models to link observed trait differentiation among populations of an

invasive species, probably arising by rapid evolution during invasion, with a niche shift toward establishment in cooler and more northerly locations. This demonstrates the importance of identifying and capturing intraspecific variation in niche responses to climate in species distribution modeling (Valladares et al. 2014). Unless these effects are understood properly, models will underestimate the potential extent of spread and invasion risk, to the detriment of invasive species risk assessment and management planning. Furthermore, current projections of climate-driven distribution shifts that do not account for intraspecific variation in traits and niches may be misleading (Early and Sax 2014, Valladares et al. 2014). We conclude that forward mechanistic distribution models have great potential for unifying studies of trait variation at the population scale with attempts to understand niche shifts and project distributions at biogeographic scales.

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