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CHOICE

The role of demography, intra-species variation, and species distribution models in species' projections under climate change

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Organisms are projected to shift their distribution ranges under climate change. The typical way to assess range shifts is by species distribution models (SDMs), which predict species' responses to climate based solely on projected climatic suitability. However, life history traits can impact species' responses to shifting habitat suitability. Additionally, it remains unclear if differences in vital rates across populations within a species can offset or exacerbate the effects of predicted changes in climatic suitability on population viability. In order to obtain a fuller understanding of the response of one species to projected climatic changes, we coupled demographic processes with predicted changes in suitable habitat for the monocarpic thistle *Carlina vulgaris* across northern Europe. We first developed a life history model with species-specific average fecundity and survival rates and linked it to a SDM that predicted changes in habitat suitability through time with changes in climatic variables. We then varied the demographic parameters based upon observed vital rates of local populations from a translocation experiment. Despite the fact that the SDM alone predicted *C. vulgaris* to be a climate 'winner' overall, coupling the model with changes in demography and small-scale habitat suitability resulted in a matrix of stable, declining, and increasing patches. For populations predicted to experience declines or increases in abundance due to changes in habitat suitability, altered fecundity and survival rates can reverse projected population trends.

Organisms may respond to climate change in a number of ways including persistence, migration, decline or extinction (Hughes 2000, Davis et al. 2005). Increasing understanding of species' responses to climate change can assist in conserving biodiversity as it provides information on the species vulnerable to climate changes and the management strategies that are likely to succeed. Species distribution models (SDMs) provide valuable tools for predicting species' responses to climate change as they project distributional changes of species' ranges under various climate scenarios (Guisan and Thuiller 2005, Thuiller et al. 2005, Elith and Leathwick 2009, Franklin 2009, Dormann et al. 2012). They have been used to ask a number of predictive questions about distributional constraints, and are often used to generate hypotheses (Dormann et al. 2012). However, they have a number of limitations, including a failure to incorporate demography (Keith et al. 2008, Lavergne et al. 2010) and the assumption that a species will respond similarly to climate change across its entire range (Pearson and Dawson 2003, Sinclair et al. 2010). Additionally, SDMs typically assume that climate alone drive shifts in species' ranges, while in reality species' responses to other changes might overshadow the impacts of shifting climate suitability (Brook et al. 2008).

Moreover, life history traits have a strong influence on the magnitude of these impacts (Regan et al. 2012, Swab et al. 2012). Recent studies integrating life history traits (Keith et al. 2008, Dullinger et al. 2012, Fordham et al. 2012), demography and physiology (Fordham et al. 2013a), or intra-specific variability (Morin et al. 2008, Bennie et al. 2010, Wang et al. 2010, Garzón et al. 2011, Fordham et al. 2013b) with SDMs have shown that increasing the complexity of models can alter predicted responses to climate change, and that accounting for species' demographic constraints can improve model predictions.

There is strong evidence that plant species often display considerable differences in vital rates across populations and have evolved ecotypes in response to environmental variation across broader gradients or even at small scales (Clausen et al. 1948, Jain and Bradshaw 1966, Waser and Price 1985, Schmitt and Gamble 1990, Galen et al. 1991, Kindell et al. 1996, Nagy and Rice 1997). Translocation experiments have shown that offspring fitness may vary among sites (Schmitt and Gamble 1990, Galen et al. 1991, Kindell et al. 1996, Nagy and Rice 1997) and that populations within a species may respond differently to climate. For example, Etterson (2007) used information from translocation experiments as

a proxy for the temporal trend of *Chamaecrista fasciculata* (Fabaceae) traits in response to changing climate, and thus projected evolutionary trajectories which suggest that the rate of evolutionary response would be slower than the predicted rate of climate change. Garzón et al. (2011) predicted the effect of local adaptation on two *Pinus* species' responses to climate change by calibrating survival rates based on translocation data. They concluded that SDM results were significantly altered by this information. Thus, there is evidence that integrating demographic information from translocation experiments and spatial information from SDMs can provide a more in-depth evaluation of the response of species to climate change. Demographic response functions have been used to link variation in environment to variation of demographic rates (Schurr et al. 2012). However, few studies have incorporated spatiotemporal demographic variability into models that predict the vulnerability of species to future climate changes. In this study, we use the observed variation in fecundity and survival across a broad geographical expanse (much of western Europe) to test potential effects of climate change on the demography and consequent population dynamics of a plant.

Spatially explicit metapopulation models can be used to make predictions of population viability under various scenarios (Akçakaya 2000). They have lately been used to incorporate life history dynamics into predictions of species' responses to shifting habitat (Keith et al. 2008, Regan et al. 2012, Swab et al. 2012). This addresses important biases of predictions through integrating factors such as fecundity, life span and dispersal with shifting patch structures. Metapopulation models can also incorporate intra-specific variability of life history traits. These advantages make this model type useful for conservation purposes and predicting vulnerabilities of species to global change (Fordham et al. 2013b). However, models typically assume the same average rates across all populations, thus ignoring differences between populations. Including empirically-based differences in average vital rates across populations adds a further level of detail to spatially-explicit population models that could reduce uncertainty in forecasts of global change on population persistence.

Information suitable for generating a spatially explicit metapopulation model was available from a reciprocal transplant experiment using *Carlina vulgaris* (Becker et al. 2006), making this species an ideal candidate for studying the importance of intra-specific variation on the response of a species to climate change. *Carlina vulgaris* is a monocarpic perennial which has been the subject of a number of studies (summarized in Becker 2005). From the translocation experiment, information was available on fecundity and survival at five different provenances, thus providing information on how vital rates changed when individuals (seeds) of each provenance were introduced to new locations. Becker et al. (2006) concluded that performance traits and individual fitness decreased with transplant distance, and attributed their findings to regional adaptation. We ask the following questions: 1) how would *Carlina vulgaris* respond to projected changes in habitat suitability due to climate change? 2) How does information on between-population variation in fecundity and survival affect predictions of the response of *Carlina vulgaris* to climate change? 3) Can intra-specific variation in

demographic rates offset or exacerbate the effects of predicted changes in habitat suitability on population viability?

Material and methods

Study species

Carlina vulgaris (Asteraceae) is a monocarpic perennial forb inhabiting sand dunes, dry grasslands, and semi-natural pastures. It is distributed across Europe and western Asia (Meusel et al. 1992). As a monocarpic perennial, individuals flower most commonly in the second year or later, and die after flowering (Klinkhamer et al. 1991). For *C. vulgaris*, there is a tradeoff between reproduction and survival, waiting another year to reproduce increases fecundity, but also increases the probability of death before reproduction (Metcalf et al. 2003). Flowering occurs between June and August, and achenes, hereafter called seeds, are dispersed during dry sunny days in late autumn, winter, or spring (Rose et al. 2002). Disturbance is important for seedling recruitment and, therefore, population dynamics (Löfgren et al. 2000). Grasslands with constant management regimes, such as grazing, have been observed to support stable *C. vulgaris* populations (Löfgren et al. 2000, Jakobsson and Eriksson 2005).

Current and future spatial distribution

To answer the question of how *Carlina vulgaris* might respond to projected changes in habitat suitability due to climate change, species distribution models were created for this species across the entire study area, western Europe. For the purpose of this study, habitat suitability refers to climatically suitable cells within areas of suitable land cover, e.g. grasslands, pasture, and sand dunes. Current climate layers with a resolution of 10 arc-minutes were obtained from WorldClim (Hijmans et al. 2005). Future climate projections with a resolution of 10 arc-minutes were obtained from the International Center for Tropical Agriculture (Ramirez and Jarvis 2008) for A1B CCCMA-CGCM31 and A2 HadCM3 for intervals ranging from 2020 through 2080. The A1B scenario, similar to RCP pathway 6.0, is of an integrated world with rapid economic growth, and thus high energy requirements balanced across a variety of fuel sources. The A2 scenario, between RCP pathways 6.0 and 8.5, represents a more divided world with regionally oriented economic development. These two scenarios were chosen as moderate representatives from the range of future climate scenarios still considered plausible.

Suitable habitat was projected using Maxent ver. 3.3.3f (Phillips et al. 2006, Phillips and Dudík 2008) in the Dismo package for R (Hijmans et al. 2011). 'Current' (interpolations of observed data, representative of 1950–2000, Hijmans et al. 2005) and future climate conditions between years 2020 and 2080 were projected using available climate projections with 10 degree grid cells (10 yr intervals for climate scenario A1B and 30 yr intervals for climate scenario A2). The six climate factors most relevant to *Carlina vulgaris* (Table 1) were used to create habitat suitability maps. Linear interpolation between time periods and projection to the

year 2100 created an annual time series of habitat suitability maps for each scenario (Anderson et al. 2009). More details of the habitat suitability model methodology is included in Supplementary material Appendix 1. Two minimum thresholds of habitat suitability were compared, equal training sensitivity and specificity (ET; threshold = 0.492; Liu et al. 2005, Freeman and Moisen 2008) and minimum training presence (MT; threshold = 0.002, Swab et al. 2012). The equal training threshold is higher, thus decreasing the amount of available suitable habitat across the landscape. The habitat suitability results were resampled from 10 arc-minutes into cells 250×250 m using the ArcMap ver. 10.0 resample function.

Available suitable habitat in each landscape was identified by using the Corine land-use map from the year 2000, also with a resolution of 250×250 m, to only include cells designated as grassland, pasture, or sand dunes, all appropriate habitat types for *Carlina vulgaris*. This land use map was overlaid on the habitat suitability maps. For all cells outside the appropriate land-use types habitat suitability was reduced to zero, otherwise cells were left unchanged.

Metapopulation model

A stochastic matrix model with three stages: dormant seeds, juveniles, and rosettes was developed for *Carlina vulgaris* (Table 2). See Supplementary material Appendix 1 for a detailed description of the parameters in the metapopulation model. Survival, fecundity, and transition values were primarily based on data from Becker et al. (2006), but amended with additional unpublished data. Fecundity was defined as the average number of offspring per individual in the reproductive stage alive at a given time step (Akçakaya 2005), and in this case represented both dormant seeds and rosettes produced, since rosettes can develop within one year. Survival, germination, and transition values were supplemented with data from the published literature. Standard deviations were calculated from the variation in these data across years. Initial abundances of 102 rosettes per cell and carrying capacity of 170 rosettes per cell (described in more detail in Supplementary material Appendix 1) were estimated using information from Jakobsson and Eriksson (2005). Juveniles were weighted as contributing 9.5% towards carrying capacity as compared with rosettes. This value was based upon differ-

Table 1. The climate factors used for the species distribution model for *Carlina vulgaris*. Factors are ordered by relative contribution to the Maxent model. Percent contribution refers to the increase in regularized gain due to a variable. Permutation importance is the drop in AUC (percentage) when a variable is removed (Phillips and Dudík 2008).

Bioclim variable	Percent contribution	Permutation importance
Temperature seasonality (standard deviation)	50.3	63.2
Maximum temperature warmest month	18	12.3
Precipitation seasonality	16.9	8.5
Minimum temperature coldest month	8.9	10.4
Annual mean temperature	4.7	1.8
Mean temperature driest quarter	1.2	3.8

Table 2. Stage matrix with average values and standard deviations for transitions between three life stages of *Carlina vulgaris* under averaged home conditions.

	Dormant seeds	Juveniles	Rosettes
Dormant seeds	0.3 ± 0.03	0	9.941 ± 8.483
Juveniles	0.0685 ± 0.0575	0	2.269 ± 1.937
Rosettes	0	0.632 ± 0.114	0.6109 ± 0.1392

ences between the maximum observed seedling abundances (Rees et al. 2006) and the maximum observed for rosettes (Klinkhamer et al. 1996), and is described in more detail in Supplementary material Appendix 1. Carrying capacity was the link between the metapopulation model and habitat suitability. When habitat suitability decreased or increased in a particular area, this was reflected by a decline or increase in carrying capacity for a patch. Patches could begin with a K of 0 if they were unsuitable initially, and increase in carrying capacity through time, begin with a high K which declined to 0, or remain suitable throughout the duration but experience changing K over time. If the population abundance exceeded K, a ceiling density dependence function reduced the population to K by the following time step.

Most seed dispersal occurs within a 10 m radius of the parent plant (Greig-Smith and Sagar 1981, Löfgren et al. 2000), and is generally limited to tens of meters (Rees et al. 2006). Seeds are equipped with a pappus and may be dispersed by wind, but the pappus easily detaches and seeds are heavy, so few seeds are dispersed over long distances (Greig-Smith and Sagar 1981, Rees et al. 2006). Thus dispersal was excluded except in a sensitivity analysis as the distance between patches is beyond 1 km.

Translocation data and region

To study how variation in fecundity and survival could affect projections of the response of *C. vulgaris* to climate change, we used demographic data collected from a translocation experiment that was performed to investigate regional adaptation in *Carlina vulgaris* (Becker 2005, Becker et al. 2006). In this experiment, individuals were reciprocally transplanted between Sweden, Germany, the Czech Republic, Luxembourg, and Switzerland, resulting in 25 combinations of origin (or home site) and growing site, including 'translocation' to the home site. Each of the 25 combinations are hereafter referred to as 'translocation scenario'. Analyses comparing the relationship between fecundity and survival rate and climate showed that subpopulations of *Carlina vulgaris* responded to translocation to different sites (Supplementary material Appendix 1, Fig. A5), but these differences were not correlated with habitat suitability. Becker (2005) and Becker et al. (2006) concluded that differences in lambda and survival rates for this species were due to regional adaptation since rosette size and other traits decreased with distance from the site of origin. However, our analysis of the translocation data indicates that, while there was variation in fecundities in response to translocation across sites, predicted fecundity (which incorporates rosette size and number of reproducing individuals) was slightly correlated ($r^2 = 0.402$) with maximum temperature of the warmest month and annual

mean temperature ($r^2 = 0.419$), and not correlated with other main climate factors predicted to be important for the species distribution (Supplementary material Appendix 1, Fig. A1). Another translocation experiment using populations within Sweden found no evidence of native superiority, but did find juvenile survival, a component not tested in Becker et al. (2006), to be 6% higher for natives at their home sites (Jakobsson and Dinnetz 2005). Though the data revealed no adaptation to climate, the translocation experiment data show that life history traits of *C. vulgaris* individuals can vary considerably when moved to different locations. Therefore, there is reason to expect variability of these traits under changing conditions.

Matrix model scenarios were developed to encompass the range of fecundities and survival rates observed in the translocation experiment. The 'home' scenario represented fecundity and survival values for *Carlina vulgaris* when individuals were planted in their country of origin, i.e. the location of provenance; metapopulation models would normally have vital rates based on this information alone. Initially, we created 25 different matrix models, one each for plants from each of the five regions when planted in each of the other regions. Growth rates associated with matrix models for many translocation scenarios were similar. Thus, we reduced the number of matrix models to fall into categories representative of the range of lambda values observed. Using observed clusters, or breaks, across the 25 lambda values of the matrices, we placed each translocation scenario into a category (Table 3). In most cases, these differences in lambda were due to differences in seed production. However, for the F5 category differences in survival rates were the main driver instead. Standard deviations were calculated from the variation in individuals from each category across years (Table 3). Given the range of intra-population variability and the weak correlation of fecundity with climate variables, we tested the entire range of fecundity (or all 5 'F' scenarios) in all regions, in addition to a home scenario at each site. Thus, in each region, each climate scenario was run with six different matrices.

The spatial distribution of *Carlina vulgaris* was divided into five separate 'regions', Germany, Switzerland, the Czech Republic, Sweden and Denmark, and Luxembourg and France, each representing an area of origin for the translocation study. Some regions included an adjacent sovereign nation in order to ensure comparable amounts of suitable habitat across the regions, e.g. Luxembourg and France. The

Table 3. Vital rates and their standard deviations for *Carlina vulgaris* rosettes in five fecundity categories. Seed and juvenile production numbers are the average number of dormant seeds or juveniles produced by any living individual per year, calculated by multiplying the proportion of individuals producing seeds or juveniles by the average number of seeds or juveniles produced by a flowering plant. Categories were delineated by expected minimum abundances.

Fecundity category	Dormant seed production	Juvenile production	Adult survival rate	Average lambda
F1	1.17 ± 1.46	0.27 ± 0.33	0.590 ± 0.004	0.88
F2	9.22 ± 0.75	2.11 ± 0.17	0.536 ± 0.051	1.58
F3	11.32 ± 3.69	2.59 ± 0.84	0.566 ± 0.049	1.72
F4	12.81 ± 4.17	2.92 ± 0.95	0.534 ± 0.013	1.78
F5	11.34 ± 4.52	2.59 ± 1.03	0.645 ± 0.147	1.76

current habitat suitability for each region was used to create two static patch structures (static ET and static MT), and future habitat suitability was used to develop dynamic patch structures based on changing climate scenarios: A1B ET, A1B MT, A2 ET, and A2 MT (described above), for a total of six climate scenarios. These patch structures were used to link the SDM results with the translocation results. Changes in habitat suitability (due to climate) were integrated into matrix metapopulation models via a dynamic carrying capacity. As habitat suitability predictions changed through time, the carrying capacity (K) per patch was recalculated. If the abundances were greater than K, vital rates were reduced until abundances were at or below K, in a manner similar to that described by Keith et al. (2008) and Swab et al. (2012). We used these six habitat scenarios to run a model with each of the five 'F' matrices for each region. For the two static climate scenarios, we also ran simulations with a home matrix as our baseline for comparison.

Simulations and scenarios

We used RAMAS GIS 5.0 (Akçakaya 2005) to link the metapopulation models with the time series of dynamic habitat suitability maps. Static patch structures, in which habitat suitability of patches remained constant through time, were used as a baseline for comparison. For each region, six habitat suitability scenarios were run with each of the five matrices, for a total of 30 different habitat (6 × 'F' matrix (5) combinations for each region (Fig. 1). This enabled us to investigate the impact of dynamic habitat suitability versus vital rates, and evaluate how the two changing simultaneously would affect projected population trends.

For each simulation, environmental and demographic stochasticity were incorporated through Monte Carlo simulations for 1500 replications over a 100 yr time period. Vital rates were uncorrelated between patches except in a sensitivity analysis. Population viability was assessed using expected minimum abundance (EMA) as a proportion of initial abundance (IA) for consistent comparison across regions. EMA is the average of the smallest population size occurring within the 100 yr time period across each of the 1500 simulations (McCarthy and Thompson 2001). The initial 10 yr of the simulation were excluded from risk calculations to allow stabilization of population dynamics. Sensitivity analyses were performed by separately perturbing initial abundances, germination, transition and survival rates, dispersal, and duration of scenario (without changes in habitat suitability) in order to determine how influential these were on species viability.

Results

Habitat suitability

Climate change predictions calculated with species distribution models (SDMs) for *Carlina vulgaris* suggest that habitat suitability will shift northward, and might increase overall depending upon the climate scenario (Fig. 2). However, most of the projected increases are in northern locations currently unsuitable and unoccupied by *C. vulgaris*. For

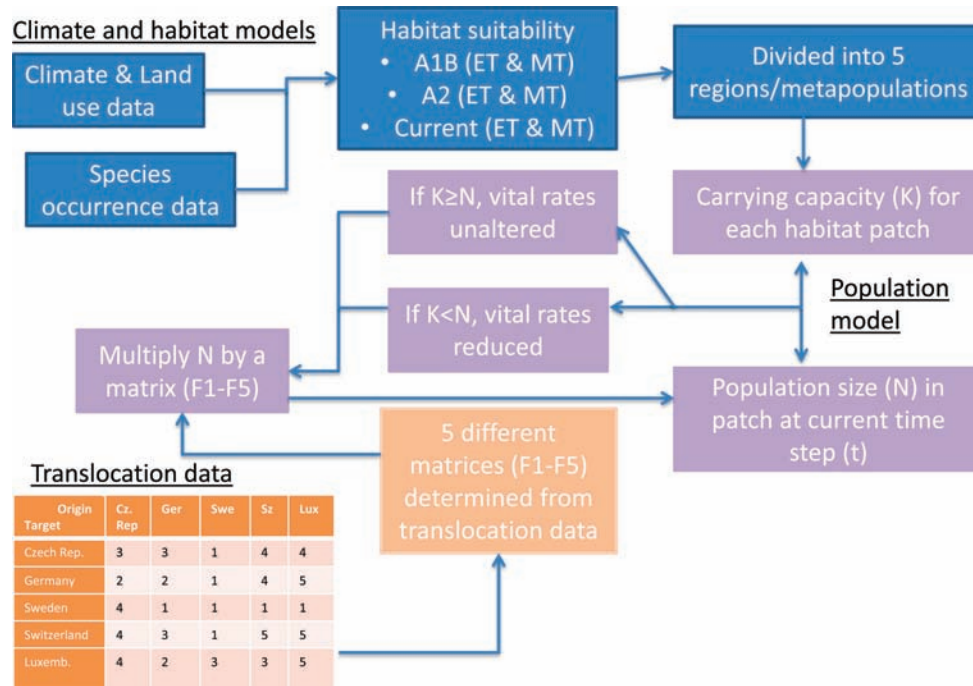


Figure 1. Coupling of habitat suitability model and stochastic population model (which integrates vital rates from translocation data). Two different thresholding decisions for the habitat suitability models were implemented, ‘ET’ or equal training, and ‘MT’ or minimum training. Each simulation runs for 100 yr, with K (carrying capacity) varying for each patch in each year but other core elements (including matrix) remaining the same. Each translocation scenario in the table was initially used to create a survival matrix. These were then grouped by expected minimum abundance into matrices termed F1 through F5, with the F5 matrix having higher minimum abundances than F1. Numbers within the translocation data table indicate the assigned matrix category for each target and origin combination. Each of the 5 regions has a total of 30 simulations, i.e. all combinations of 6 habitat suitability scenarios and 5 different ‘F’ matrices. Modified from Keith et al. (2008).

three of the five translocation sites, habitat suitability is predicted to decrease, especially under the more influential A2 scenario (Supplementary material Appendix 1, Fig. A6). Additionally, most of the climate factors considered to be the most influential on the species’ distribution (temperature seasonality, max temperature of the warmest month, precipitation seasonality) are predicted to change at these locations (Supplementary material Appendix 1, Fig. A7).

Results from habitat suitability maps show that threshold selection can have a large impact on projections of the amount of suitable habitat, as reflected in changes in carrying capacity (K) through time (Supplementary material Appendix 1, Fig. A6). Particularly for populations in Sweden and Denmark, suitable initial habitat is significantly lower when the threshold for habitat suitability is based upon the higher equal training sensitivity and specificity value.

Intra-specific variability and habitat suitability

As fecundity (and therefore lambda) increases, from category F1 to F5, the expected minimum abundance (EMA) relative to initial abundance (IA) also increases (Fig. 3). Populations with the lowest fecundities (F1) are predicted to become extirpated under all climate scenarios. However, fecundity increases above the F2 category do not increase the EMA/IA ratio, and for these categories habitat suitability seems to be the main driver of minimum population abundances (Fig. 3).

When comparing results from fecundity categories with the home fecundity (i.e. fecundity of plants when grown in their home location), EMAs can increase or decrease depending on the climate scenario. When both fecundity and habitat suitability decrease, EMAs decrease 100% of the time (Table 4). However, even when fecundity and HS both increase, EMA is lower 37.5% of the time. When one factor increases and the other decreases, results are mixed (Table 4).

The A2 climate scenario is generally bad for the species. Under the A2 climate scenario our models predict declines to, or close to, extirpation for most regions except Sweden and Switzerland under the MT threshold, regardless of fecundity rate (Fig. 3). For the A1B scenario, when habitat declines are proportionally small, as predicted for Germany and Switzerland (Supplementary material Appendix 1, Fig. A6), or habitat increases are predicted to be in new areas unpopulated currently by *C. vulgaris*, and unreachable by dispersal as in Sweden, EMA/IA ratios are generally unaffected by climate scenario or threshold for occupancy (Fig. 3). However, when habitat declines are predicted to be dramatic, as for Luxembourg and France (Supplementary material Appendix 1, Fig. A6), we predict population declines under climate change, i.e. decreases in EMA and the proportion of EMA/IA (Fig. 3). For the Czech Republic, where increases in habitat suitability are predicted in currently occupied patches, climate change is predicted to increase EMAs dramatically under the high threshold A1B scenario.

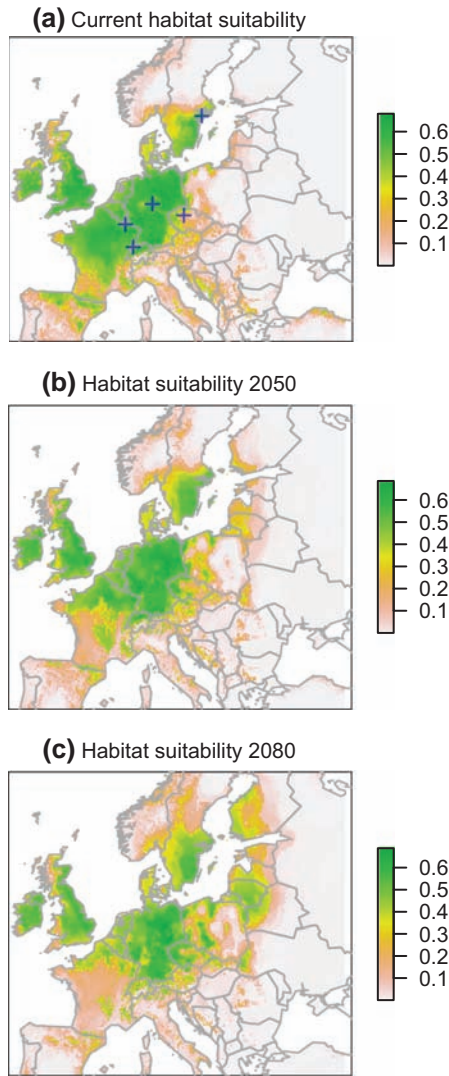


Figure 2. Predicted habitat suitability for *Carlina vulgaris* with (a) current climate (b) predicted climate in 2050 under scenario A1B (c) predicted climate in 2080 under scenario A1B. Greener colors indicate increasing suitability of habitat. Plus symbols indicate translocation sites.

Sensitivity analysis of life history traits shows that the model is most sensitive to changes in scenario duration, production of juveniles by rosettes, and transition between juvenile and rosette stages (Supplementary material Appendix 1, Table A1). It is less sensitive to changes in survival rates for the rosette stage, and insensitive to changes in other parameters such as seed production. Varying the initial abundance to K ratio only affects EMA when the IA is reduced to 10% of the baseline IA, and has a greater impact on models with lower fecundities (Supplementary material Appendix 1, Table A1). Seed production for higher fecundity categories is so high that after 10 yr there is minimal difference in abundances between scenarios with lower initial abundances and those with higher initial abundances, indicating that this species is limited more by available sites than by seed supply. Dispersal makes no difference for most scenarios, including all minimum threshold models. Five landscape configurations resulted in a positive influence of dispersal

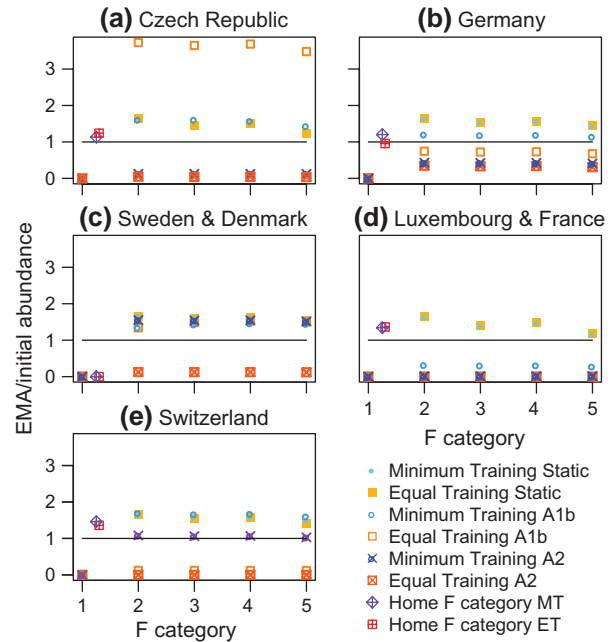


Figure 3. Expected minimum abundance (EMA)/initial abundance for *Carlina vulgaris* metapopulations in (a) the Czech Republic, (b) Germany, (c) Sweden and Denmark, (d) Luxembourg and France, and (e) Switzerland for various threshold selections and under a static climate and changing climate using A1B and A2 predictions. The solid black line indicates the point at which EMA equals initial abundance.

(Supplementary material Appendix 1, Fig. A8). Sweden and Denmark for A1B or A2 ET scenarios, and Switzerland under the A1 ET scenario showed the largest increases in EMA/IA, due to colonization of newly available patches when dispersal occurred. Correlation of environmental stochasticity in vital rates between patches did not affect results.

Discussion

Species distribution models (SDMs) project increases, declines, or shifts in suitable habitat for species under climate change (Franklin 2009). For *Carlina vulgaris*, SDMs project an increase in the overall amount of suitable habitat under

Table 4. Percentage of scenarios with increases (+) or decreases (–) in EMA for *Carlina vulgaris* metapopulation model results given increases (+) or decreases (–) in fecundity and habitat suitability (HS). Increases or decreases in EMA are as compared with the EMA for a similar scenario, but with stable habitat and home fecundity values.

		Fecundity	
		+	–
HS	+	62.5%+	25%+
	–	37.5%–	75%–
	+	57%+	0%+
	–	43%–	100%–

climate change (Fig. 2). When this is translated into changes in carrying capacity for specific locations (VanDerWal et al. 2009), however, some locations are projected to experience large declines in abundances, while increases are projected for other locations (Supplementary material Appendix 1, Fig. A6). Incorporating spatial variability of vital rates into predictions of the species' response to climate change impacts model predictions. When life history variables such as fecundity or survival rates change, this can result in increases in population viability even in the face of decreasing habitat suitability (Table 4). Overall, the results of this study indicate that for *Carlina vulgaris*, population models provide different insights into species' responses to climate change than SDMs alone. This is an underappreciated insight, although it has been emphasized previously that SDMs ignore life history traits, adaptation, and plasticity of individuals has often been considered a limitation of SDMs (Pearson and Dawson 2003, Dormann 2007, Keith et al. 2008, Elith and Leathwick 2009). It is necessary to integrate studies investigating intra-specific variation in demographic traits of species with SDMs, as in this paper, in order to fully understand the potential responses of species to climate change.

Several main findings emerge from the research, discussed in more detail below: 1) projected increases or decreases in habitat suitability do not always correspond with increases or decreases in expected minimum abundances. 2) Habitat suitability thresholding decisions can affect predictions of species viability. 3) *Carlina vulgaris* is sensitive to extreme declines in fecundity, but not to increases.

Habitat suitability and expected minimum abundance

When projected habitat suitability increases, expected minimum abundance (EMA) sometimes increases and sometimes decreases as compared with scenarios with stable habitat (Table 4, Fig. 3). This can be due to changes in fecundity, as the effects of decreased fecundity outweigh the effects of increases in habitat suitability, especially if the increases are in previously unoccupied patches. In some cases (for one, where both fecundity increases and habitat suitability increases by the end of the simulations), the point of lowest habitat suitability is in the middle of the time period. These lows in habitat suitability can cause decreases in EMA. Subsequent increases in habitat suitability (often in new patches) are not capitalized upon due to limited dispersal. Most studies look at habitat suitability in 30 yr intervals (Pearson and Dawson 2003). Results with low EMAs despite overall increases in habitat suitability indicate that simply looking at habitat suitability at a few time periods can be an oversimplification resulting in an underestimate of the vulnerability of the species to climate change. Additionally, increases in fecundity can compensate for decreases in habitat suitability – for example, in 57% of the model scenarios EMA increased when habitat suitability decreased and fecundity increased (Table 4). Since the results show that changes in habitat suitability and fecundity interact to affect the species' response to climate change, this indicates that adding complexity by coupling population models with SDMs can change direction and magnitude of predictions.

Habitat suitability thresholding decisions can affect predictions of species viability

Expected minimum abundance values were influenced by the choice of threshold for habitat suitability. However, while threshold was important to absolute numbers of projected population declines, it only occasionally affected results when using EMA/initial abundance (Fig. 3). This suggests that habitat suitability threshold decisions can affect predictions of species viability if absolute values of population declines are of interest, whereas the ranking of scenarios (in this case regions and fecundity classes) appear to be robust to training thresholds.

Sensitivity of *Carlina vulgaris* to changes in fecundity

In populations with high fecundity (fecundity categories F2–F5), the expected minimum abundance of *Carlina vulgaris* seemed to be driven primarily by the coefficient of variation, rather than by average fecundity (Fig. 3). The most likely explanation for this result is that, for the focal species, seed production is comparatively high and availability or limitation of recruitment microsites is the main driver of population size within suitable patches. In the model, this was reflected by the fact that for the F2–F5 fecundity categories, average population abundances were at carrying capacity for most simulations. Thus, minimum abundances were driven by years of low seed production. The results indicate that variable fecundity will minimally impact this species, typically only if fecundity is so low as to result in population growth rates below 1.

For the study species, changes in fecundity and survival rates were not correlated with changes in habitat suitability as predicted by SDMs or with changes in environmental variables predicted to be important by SDMs. This indicates that the two evaluations of species' responses to climate change – translocation experiments and SDMs – are capturing different processes, SDMs are incorrect in their predictions, or the difference in scale between climate predictors used in SDMs and local climate relevant to translocation experiments makes it difficult to integrate the two. Species distribution models tend to take into account processes affecting species at large scales (Elith and Leathwick 2009), using the entire species distribution to predict changes in habitat suitability (but see Sork et al. 1993). Translocation studies generally evaluate life history trait responses to environmental properties at local scales (Becker et al. 2006, Bischoff et al. 2006), focusing on how individual plants will perform in novel climates within the species range (Becker et al. 2006). Thus while predictions of the SDMs provide insight into the effects of climate change on a species' distribution at the larger scale, translocation experiments capture responses of individuals at local scales where plants may respond more directly. This study integrates both scales, and results show that factors at both scales can influence results. Current difficulties in dealing with scale disparities when fitting SDMs (Elith and Leathwick 2009) can potentially be addressed using this methodology.

Because we did not find a strong correlation of fecundity with climate variables, the results of the translocation experiment

coupled with the population models merely provide bounds on plausible population responses to novel climate and habitat shifts. However, given that intra-specific variation of life history characters influenced results, this study shows that translocation experiments can increase understanding of species responses to climate change. If projected future climate conditions at some locations are similar to current climate at translocation sites, information from the translocations can be used to predict how populations will respond to climate change. Even if projected future climatic conditions are novel, information from the translocation experiment can still reveal when, or why, the species might not respond to climate change as a whole. However, given the amount of work required for these experiments, this would best be done for representatives of functional groups to determine which vital rates are most significant and/or most likely to be affected by climate change. Combining these experiments with models as done in this study can be an effective means of determining how and to what extent changes in vital rates will affect populations.

The limitations of species distribution models have been well studied in the literature (Pearson and Dawson 2003, Franklin 2009, Lavergne et al. 2010), and the limitations of combining SDMs with metapopulation models have also been addressed (Keith et al. 2008, Lawson et al. 2010, Regan et al. 2012, Swab et al. 2012). Adding new components to this modeling platform compounds uncertainty in results. Uncertainty in the model parameters is high given that the translocation experiment followed one cohort for three years in each of the translocation scenarios, and thus year-to-year environmental variability in vital rates is based on only two years for the larger life stages. If the annual environmental variation in survival rates was under-estimated due to the short duration of the experiment, survival rates could have a larger influence on the population viability overall. Fecundity and germination rate, however, are unlikely to affect the species unless they are low enough that population growth rates are below one. Furthermore, the translocation study did not capture viable population dynamics for plants from Sweden, whether at home or away, and therefore in simulations the Swedish-based matrices resulted in extirpation under all scenarios including static habitat suitability. Since there are currently *Carlina vulgaris* populations persisting in Sweden, it is clear that there is a missing factor. Dispersal is another limitation of the model. Since dispersal for this species is thought to be only tens of meters (Rees et al. 2006), baseline simulations did not include dispersal despite the fact that rare long distance dispersal is thought to be important to plant population dynamics (Nathan 2006). However, for this species, it is unlikely that new patches will be colonized within a decade and model results including dispersal reflected this. Finally, there is inherent uncertainty in the habitat suitability models, and linear interpolating between time slices, in particular extrapolating beyond year 2080 adds uncertainty to the simulations. The projections are not guided by emissions scenarios post 2080, and therefore the projected changes in carrying capacity are only useful in terms of understanding the species response to changes in habitat suitability, rather than being applicable to the species likely response to climate change. Overall, the results were fairly robust to perturbations in the demographic parameters as demonstrated in the sensitivity analyses (Supplementary material Appendix 1, Table A1), indicating that the general trends of the results

are likely to be the same even if there are small changes in life history parameters.

Though the number of climate model scenarios was limited to two, the SDM provided a useful platform for comparing the response of the species to climate changes under various scenarios of decreasing, increasing, and shifting habitat suitability. Land use change will likely also occur with climate change, potentially further reducing habitat availability, resulting in overly optimistic projections of habitat (Thomas et al. 2004, Pressey et al. 2007). Overall, this study should be taken as an attempt to increase our understanding of species vulnerabilities to climate change rather than one predicting the outcome for *C. vulgaris*.

Species distribution models capture part of the response of species to climate change, but do not reflect all potential responses to climate change (Keith et al. 2008, Lawson et al. 2010, Swab et al. 2012). Coupling life history traits and spatially explicit population dynamics with SDMs allows us to see when changes in habitat suitability will result in changes in abundance across the landscape for the species – not all declines in habitat suitability necessarily lead to declines in populations because they may be accompanied by positive changes in a vital rate. However, if habitat suitability were to continue to decline, it is likely that the beneficial effects of increases in demographic rates will ultimately be outweighed by the reduction in suitable habitat in the long run, provided suitable habitat predictions are a good reflection of carrying capacity and hence population survival. Translocation studies often attempt to capture differences between populations in life history traits (Kawecki and Ebert 2004). This study shows these differences may indeed impact species responses to climate. Changes in fecundity, because of plasticity or adaptation, might result in a tempering of the effect of climate change on population predictions if areas with predicted declines in habitat suitability experience increases in fecundity. This is an indication that while species distribution modeling is a valuable tool for predicting species' responses to climate change, integrating these with population models parameterized with information from translocation studies can provide a fuller picture of overall projected trends.

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Supplementary material (Appendix ECOG-00585 at <www.ecography.org/readers/appendix>). Appendix 1.