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Addressing potential local adaptation in species distribution models: implications for conservation under climate change

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Abstract. Species distribution models (SDMs) have been criticized for involving assumptions that ignore or categorize many ecologically relevant factors such as dispersal ability and biotic interactions. Another potential source of model error is the assumption that species are ecologically uniform in their climatic tolerances across their range. Typically, SDMs treat a species as a single entity, although populations of many species differ due to local adaptation or other genetic differentiation. Not taking local adaptation into account may lead to incorrect range prediction and therefore misplaced conservation efforts. A constraint is that we often do not know the degree to which populations are locally adapted. Lacking experimental evidence, we still can evaluate niche differentiation within a species' range to promote better conservation decisions. We explore possible conservation implications of making type I or type II errors in this context. For each of two species, we construct three separate Max-Ent models, one considering the species as a single population and two of disjunct populations. Principal component analyses and response curves indicate different climate characteristics in the current environments of the populations. Model projections into future climates indicate minimal overlap between areas predicted to be climatically suitable by the whole species vs. population-based models. We present a workflow for addressing uncertainty surrounding local adaptation in SDM application and illustrate the value of conducting population-based models to compare with whole-species models. These comparisons might result in more cautious management actions when alternative range outcomes are considered.

Key words: biodiversity management; conservation effectiveness; environmental niche models; intraspecific variation; *Lycaeides melissa samuelis*; model uncertainty; *Primula nutans* var. *finmarchica*; translocation.

INTRODUCTION

Correlative species distribution models (SDMs) are used for inferring relationships between species and their environment. They are commonly applied in ecological studies, often to describe species' niches and to inform conservation planning (Bakkenes et al. 2002, McCormack et al. 2010, Morueta-Holme et al. 2010, Renwick et al. 2011, Schwartz 2012, Guisan et al. 2013). Their use has recently increased due to the improved availability of data on species occurrences and projected climate (e.g., Global Biodiversity Information Facility [*data available online*]⁷ and WorldClim [Hijmans et al. 2005]), as well as the development of new software platforms and algorithms to analyze and synthesize these data (Franklin 2010).

SDMs (also called niche, envelope, or bioclimatic models) have been criticized for simplifying or omitting factors that influence the distribution of species, such as traits controlling dispersal ability and biotic interactions, and for assumptions of niche conservatism and of the species being in ecological equilibrium with its environment (Guisan and Zimmermann 2000, Dormann 2007, Araújo and Peterson 2012, Early and Sax 2014). Several of these shortcomings have been acknowledged and investigated, including the importance of choosing the right modeling algorithm, sample size, and environmental variables for an accurate prediction of the distribution (Stockwell and Peterson 2002, Heikkinen et al. 2006, Austin and van Niel 2011, Synes and Osborne 2011). These limitations, and the importance of drawing appropriate conclusions from SDM results, need to be addressed, especially when predicting future suitable areas for a species and using SDMs for planning conservation measures (Pearson and Dawson 2003, Heikkinen et al. 2006, Dormann 2007, Franklin 2010, Araújo and Peterson 2012).

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⁷ <http://www.gbif.org/occurrence>

One potential source of error in SDMs that has been largely overlooked is the effect of local adaptation and the consequences of functional differences among populations within a species' ranges. A common approach in ecological analyses, including SDMs, is to assume that all populations of a species respond homogeneously to the range of environmental conditions experienced by the whole species (Davis and Shaw 2001, Bolnick et al. 2003, Atkins and Travis 2010, Banta et al. 2012, Fitzpatrick and Keller 2015). However, species vary genetically across their range and populations can be locally adapted with specialized climatic or other environmental tolerances. If an SDM is constructed using distribution data for the whole species, it will also treat the species as an evolutionarily homogeneous entity over its entire range (Hampe 2004) and therefore not take into account possible population differences, including local adaptation.

Several studies indicate that populations of some species are adapted to local conditions (Davis and Shaw 2001, Bolnick et al. 2003, Fournier-Level et al. 2011, Banta et al. 2012), including climate (Pelini et al. 2009, O'Neil et al. 2014). Attempts have recently been made to incorporate local adaptation and phenotypic plasticity into SDMs when modeling suitable habitats under climate change (Pearman et al. 2010, Benito Garzón et al. 2011, Banta et al. 2012, Bocedi et al. 2013, Oney et al. 2013, Romero et al. 2013, Homburg et al. 2014, Valladares et al. 2014) and studies indicate that there can be an effect, although varying in magnitude and direction, of discriminating among populations in the modeling process.

This does not, however, mean that one should always assume local adaptation in SDMs if populations of species occupy apparently different environments, since they may be phenotypically plastic. Nevertheless, without extensive experiments, we cannot know whether observed environmental differences among populations have led to local adaptation (Kawecki and Ebert 2004, Pelini et al. 2009, Vergeer and Kunin 2013, Kreyling et al. 2014, O'Neil et al. 2014). While mechanistic or individual-based process models can offer more detailed insight on environmental requirements of species (*sensu* Morin and Thuiller 2009), they also require species-specific physiological parameters that are rarely available. Thus, we need additional cost- and time-effective methods for testing the potential importance of population differences. Such first-order approximations based on simplified assumptions can serve as a basis for refined investigations requiring more time and resources. Previous studies have not compared the potential magnitude of difference among populations that might lead us to model populations separately when using SDMs nor the conservation implications of incorporating or ignoring local adaptation in SDMs.

Here, we use two case species to address the following questions: (1) Does modeling geographically disjunct populations separately significantly alter SDM projections compared to projections based on whole species analyses?

(2) Does considering population differences affect conservation recommendations and conservation strategies? and (3) Can climatic variables inform subsequent field experiments to detect and measure local adaptation?

METHODS

Study species

The Karner blue butterfly (*Lycaeides melissa samuelis*; KBB) occurs in the Great Lakes and nearby regions of North America, historically ranging from Minnesota, USA, in the west to New Hampshire, USA, in the east (Grundel et al. 1998, Forister et al. 2010). It is a federally listed endangered species in the USA whose larvae feed on leaves of a single plant species, wild lupine (*Lupinus perennis*). The KBB has declined, in part, because its main habitats, savannas and barrens, have been anthropogenically altered since the 19th century (Forister et al. 2010). Populations are currently found in Wisconsin, Michigan, and New York, have likely been recently extirpated in Minnesota, Illinois, Indiana, and Ontario, and have recently been reintroduced into Ohio and New Hampshire (Fig. 1a). KBB populations have been shown to be genetically different, at least in their mitochondrial haplotypes (Gompert et al. 2006).

The Siberian primrose (*Primula nutans*) is a circumpolar, perennial plant that mainly grows in seashore and riverside meadows (Mäkinen and Mäkinen 1964, Kreivi et al. 2011). The subspecies *P. nutans* ssp. *finmarchica* occurs in northern Europe (Kreivi et al. 2006). Mäkinen and Mäkinen (1964) divided this subspecies into two varieties according to morphological and ecological characteristics: *P. nutans* var. *finmarchica* occurs at the shores of the Arctic Sea, while *P. nutans* var. *jokelae* occurs by the Bothnian Bay in Finland and Sweden and by the shores of the White Sea in Russia. However, recent genetic studies have found the three main populations of the Siberian primrose (SP) to be similarly distinct from each other (Kreivi et al. 2011).

Both taxa are threatened and occur in geographically separated populations with little gene flow among populations (Gompert et al. 2006, Kreivi et al. 2006). The main populations of both species were possibly separated into their geographically distinct populations during the last glacial retreat (Mäkinen and Mäkinen 1964, Gompert et al. 2008). Further, they have been sufficiently studied (Grundel et al. 1998, Gompert et al. 2006, Rautiainen et al. 2009, Kreivi et al. 2011) to provide distributional data and biological information useful in niche model interpretation. However, we do not know if populations of these species are locally adapted.

Occurrence data

Occurrence data for the KBB (Fig. 1a) were combined from site survey records, museum records, individual collector records, and GBIF data (see footnote 7), giving us 828 unique occurrence points. For SP distribution

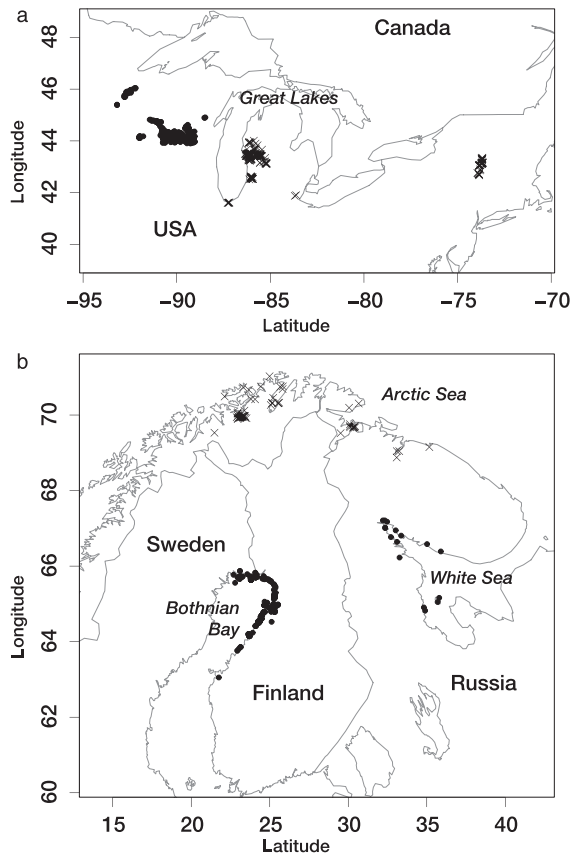


FIG. 1. Occurrence points were broken up into populations as determined by PCA, see *Methods: Grouping of populations* and *Results*. (a) Symbols are x, KBB-East population; circle, KBB-West population. (b) Symbols are x, SP-North population; circle, SP-South population. The whole species models used all occurrence points of each species (KBB-Whole and SP-Whole).

data (Fig. 1b), we combined the occurrence data obtained from GBIF, Kastikka (Finnish plant distribution database; Lampinen et al. 2012), and Hertta (Finnish Environment Institute, *unpublished data*), as well as information on occurrences in Russia based on herbarium specimens (from collections in Helsinki [H] and Turku [TUR]; acronyms after Thiers, *available online*).⁸ We also added some distribution points in Russia according to the distribution map by Hultén and Fries (1986), giving us 210 occupied cells. For both species, one grid cell (30 arcsec) was either occupied or not, irrespective of whether many occurrence points fell into a specific grid cell.

Study region

We created the study domain using a 1000-km buffer around the occurrence points for each species. This mask included all occurrences of the species yet lessened extrapolation, i.e., estimation outside observed conditions, when projecting into other climate conditions and

larger domains, and excluded bioclimatic regions that were spuriously similar to where the species occurred. A common recommendation for choosing the study area is to include areas to which the species could disperse (Merow et al. 2013). In this study, we considered conservation under climate change, including possible use of assisted migration to move species to climatically suitable regions (McLachlan et al. 2007, Hällfors et al. 2014). As a consequence, we not only needed to consider areas where the species could disperse to on its own in the near future, but also areas where it might migrate under longer climate changes and sites that might be candidates for assisted migration (also called managed relocation).

Climatic data

Data on current climatic conditions (average climate for 1950–2000; Hijmans et al. 2005), represented by 19 bioclimatic variables, were obtained from the WorldClim dataset (Hijmans et al. 2005). The spatial resolution of both the current and future climate data was 30 arcsec. Future climate data were obtained from CCAFS (Climate Change, Agriculture and Food Security; Ramirez and Jarvis 2008). This dataset has been statistically down-scaled from climate models for the Fourth report of the International Panel for Climate Change (IPCC 2007). The Fifth IPCC report (IPCC 2014) contained updated climate projections; however, the climate projection data available at 30-arcsec spatial resolution were not available for multiple decades. We used seven time periods during the 21st century to generate future distribution projections. Each time frame or decade corresponded to a 30-yr average, e.g., 2040s is given by 2030–2059. We used predictions for future climate calculated according to the UKMO-HadGEM1 general circulation model and the A1B scenario, which were the most recent climate scenarios available at the time we conducted this present study (Nakicenovic and Swart 2000). This scenario describes a world with rapid economic growth using both fossil and non-fossil energy, and reflects current CO₂ growth rates (Le Quéré et al. 2009).

We performed a variance inflation factor analysis (VIF) to help eliminate highly correlated variables as SDM predictors (Merow et al. 2013). Although machine learning methods such as MaxEnt can cope with some degree of collinearity (Elith et al. 2011), we elected to use variable importance and response curves to inform future experiments (see study question 3 in *Introduction*). If two environmental variables are highly correlated, the marginal response curves can be misleading. Therefore, we excluded correlated variables prior to calibrating models. For the analysis, we calculated Pearson's correlation values for all 19 bioclimatic variables from a sample of 100,000 locations within both study regions (see Appendix S1: Table S1 for correlation values). We then ran an ordinary least squares regression that held one variable as dependent and all the other variables as explanatory. We calculated variance inflation factors (VIF) for each variable and subsequently deleted the

⁸ <http://sweetgum.nybg.org/ih/>

variable with the highest VIF value if it was greater than 10 and repeated the whole procedure until all VIF values were less than 10 (Craney and Surles 2002, O'Brien 2007). We retained eight variables for each species (Table 1).

Grouping of populations

We used principal components analysis (PCA; Abdi and Williams 2010) to explore whether occurrences of the species are segregated by climatic variables and to identify potential climatically distinct populations. We used the PCA function in the R package FactoMineR (Lê et al. 2008) to calculate principal components using the entire set of 19 variables. We used the first two principal components and the 95% confidence interval of clustering, together with knowledge of the taxonomy and the spatial genetic structure of the species (Gompert et al. 2006, Kreivi et al. 2011), to define the populations for this study. KBB occurrence points were divided into western and eastern populations (KBB-West and KBB-East; *Results*; Fig. 1) and the SP into southern and northern populations (SP-South and SP-North; Fig. 1). The whole species are referred to as KBB-Whole and SP-Whole. To inform our third research question, which aimed to identify key climatic variables that differed between populations and to inform experiments testing local adaptation, we also conducted PCA using uncorrelated climatic variables.

Constructing SDMs

We constructed separate SDMs for the two populations of each species (KBB-East, KBB-West, SP-South, and SP-North) in addition to an SDM for each species as a whole (KBB-Whole and SP-Whole). Models differed in number of distribution points (KBB-Whole, 828; KBB-East, 355; KBB-West, 473; SP-Whole, 210; SP-South, 150; and SP-North, 60). Different sample sizes may affect the comparison of models. However, removing information through data point deletion is not necessarily a robust alternative and does not eliminate the need to model populations separately if they are locally adapted.

We used MaxEnt (Phillips et al. 2006) to model species distributions, as it is a commonly used SDM algorithm for presence-only data (Franklin 2010, Merow et al. 2013), and it has also been shown to perform well in comparisons among different algorithms (Elith et al. 2006, Franklin 2010). Although ensemble approaches in SDM have recently been favored (Araújo and New 2007), we used one algorithm, one set of climatic parameters, and one climatic projection based on one general circulation model and one carbon emissions scenario. This enabled us to concentrate on the differences that the species vs. population approaches produced.

We used 20% of the occurrence data for testing the models. We used ten-fold cross validation, thus

TABLE 1. Index for variable abbreviations and table of variable importance (permutation importance in MaxEnt model) of variables included in each model.

Variable			KBB-Whole	KBB-East	KBB-West	SP-Whole	SP-North	SP-South
AMT	bio1	Annual mean temperature	4.8	19	10.3
MDR	bio2	Mean diurnal range	1.4	1.2	1.7	2.7	1.3	5.9
IT	bio3	Isothermality	0.9	0.5	0.6
TS	bio4	Temperature seasonality	9.6	11.2	1.9
TWAM	bio5	Max. temperature of warmest month
TCM	bio6	Min. temperature of coldest month
TAR	bio7	Temperature annual range
TWeQ	bio8	Mean temperature of wettest quarter	4.5	16.9	1.8	1	6.3	2.5
TDQ	bio9	Mean temperature of driest quarter	4	12	1.4	27.3	57.4	1.1
TWaQ	bio10	Mean temperature of warmest quarter	70.5	27.9	47.9
TCQ	bio11	Mean temperature of coldest quarter
AP	bio12	Annual precipitation
PWeM	bio13	Precipitation of wettest month	2.2	7	2.4
PDM	bio14	Precipitation of driest month
PS	bio15	Precipitation seasonality	6.2	12.6	40.3	0.4	0.3	0.9
PWeQ	bio16	Precipitation of wettest quarter
PDQ	bio17	Precipitation of driest quarter
PWaQ	bio18	Precipitation of warmest quarter	1.7	11.2	2.7	62.1	14.5	75.9
PCQ	bio19	Precipitation of coldest quarter	0.9	0.7	2.7

Note: Variable importance higher than 20 in bold.

obtaining 10 models and 10 projections for each species. We converted the probability of habitat suitability to binary outputs of suitable and unsuitable areas using the optimal threshold of maximum sensitivity plus specificity, striking a balance between sensitivity and specificity (Liu et al. 2005). For each species and population, this was conducted for all 10 models, giving us 10 presence-absence maps. We then used a majority vote approach to determine the final presence-absence map: the cell was considered suitable in the final map if more than five models predicted it to be suitable. The model performance was checked using the area under the receiver operating characteristics curve (AUC; Jiménez-Valverde 2012) for the ten models used to obtain one consensus prediction. We report the mean and standard deviation of AUC for each suite of ten models (see *Results*). Since we were not comparing the performance of different models, this measure was suitable for our purpose, although concerns have been recognized for using AUC as the only measure of model performance (Lobo et al. 2008).

To understand which climatic variables may be important and differ by population (see study question three in *Introduction*), we used the permutation importance measure in MaxEnt to assess the relative contribution of each environmental variable in determining the predicted distribution of the modeled entity (Phillips 2006). Response curves of each variable indicate the response of the species (or population) to different variable values (Phillips 2006), i.e., the relative probability that a cell with a certain variable value is suitable for the modeled entity. We identified and examined response curves of the most important variables in the models and PCA.

Niche similarity tests

To inform study question one (see *Introduction*) and evaluate the representativeness of the whole-species models for identifying suitable conditions for each population and whether this changed over time, we performed a niche similarity test. Using ENMTools (Warren et al. 2008, 2010), we measured niche similarity between the mean probabilities of occurrence from ten-fold cross validation under all time periods of all three models for both species. We quantified niche similarity using two measures: Schoener's D (Schoener 1968) and the *I* statistic (a derivative of Hellinger's distance; see Warren et al. 2008, 2010 for additional details). Both metrics range from 0 (species have completely discordant niches) to 1 (species have identical niches). High values of these metrics between the predictions of the whole-species model and that of the two population models indicate that they are predicting different areas of future occupancy. Changes in the metrics over time illustrate the degree to which the whole species model can or cannot represent the climatic niches of the constituent populations.

Evaluation of conservation implications

To evaluate the effects of the two approaches (modeling species as a whole or populations separately) on conservation decisions (see study question two in *Introduction*), we used the binary suitability maps (suitable vs. unsuitable cells; Figs. 3a and 4a; Appendix S1: Fig. S2) to devise broad conservation plans. We compared the negative and positive effects of possible conservation decisions made under climatic local adaptation of populations vs. the species not being differentiated into populations, assuming we knew which phenomenon was correct and which incorrect.

RESULTS

Delineating populations

KBB showed distinct clustering in PCA (Fig. 2a; variable contribution in Appendix S1: Table S2), and we divided the KBB occurrences into two populations according to this. Two distinct groups were identifiable: the eastern population (KBB-East) consisted of occurrences in Illinois, Indiana, Michigan, Ohio, New York, and New Hampshire in the USA and Ontario of Canada. The western population (KBB-West) consisted of occurrences in Minnesota and Wisconsin (Figs. 1a and 2a). No single variable dominated the PC1 axis (all contributed <10%; Appendix S1: Table S2) whereas the PC2 axis was dominated by temperature of warmest month (TWaM), temperature of warmest quarter (TWaQ), and temperature of wettest quarter (TWeQ; together contributing >50% of the PC axis; index of abbreviations in Table 1).

The SP occurrences did not form clusters that were as well separated (Fig. 2b; variable contribution in Appendix S1: Table S2). However, some clustering was apparent on the combination of PC1 (dominated by and contributing with >50%: precipitation seasonality [PS], precipitation of coldest quarter [PCQ], precipitation of driest quarter [PDQ], precipitation of driest month [PDM], and annual mean temperature [AMT]) and PC2 (dominated by and contributing with >50%: temperature annual range [TAR], temperature seasonality [TS], and mean diurnal range [MDR]). This clustering loosely follows the taxonomic division of the varieties (Mäkinen and Mäkinen 1964). Additionally, there is probably minimal gene flow among the geographically distinct populations (by the Bothnian Bay, White Sea, and Arctic Sea; Kreivi et al. 2011). Therefore, we chose not to assign occurrences from the same geographic area to separate populations for the study. We grouped them into the southern and northern populations, which corresponded to var. *jokelae* (occurrences by Bothnian Bay and White Sea) and var. *finmarchica* (occurrences by the Arctic Sea), respectively (Fig. 1b; SP-South and SP-North, respectively). Although SP populations could have been

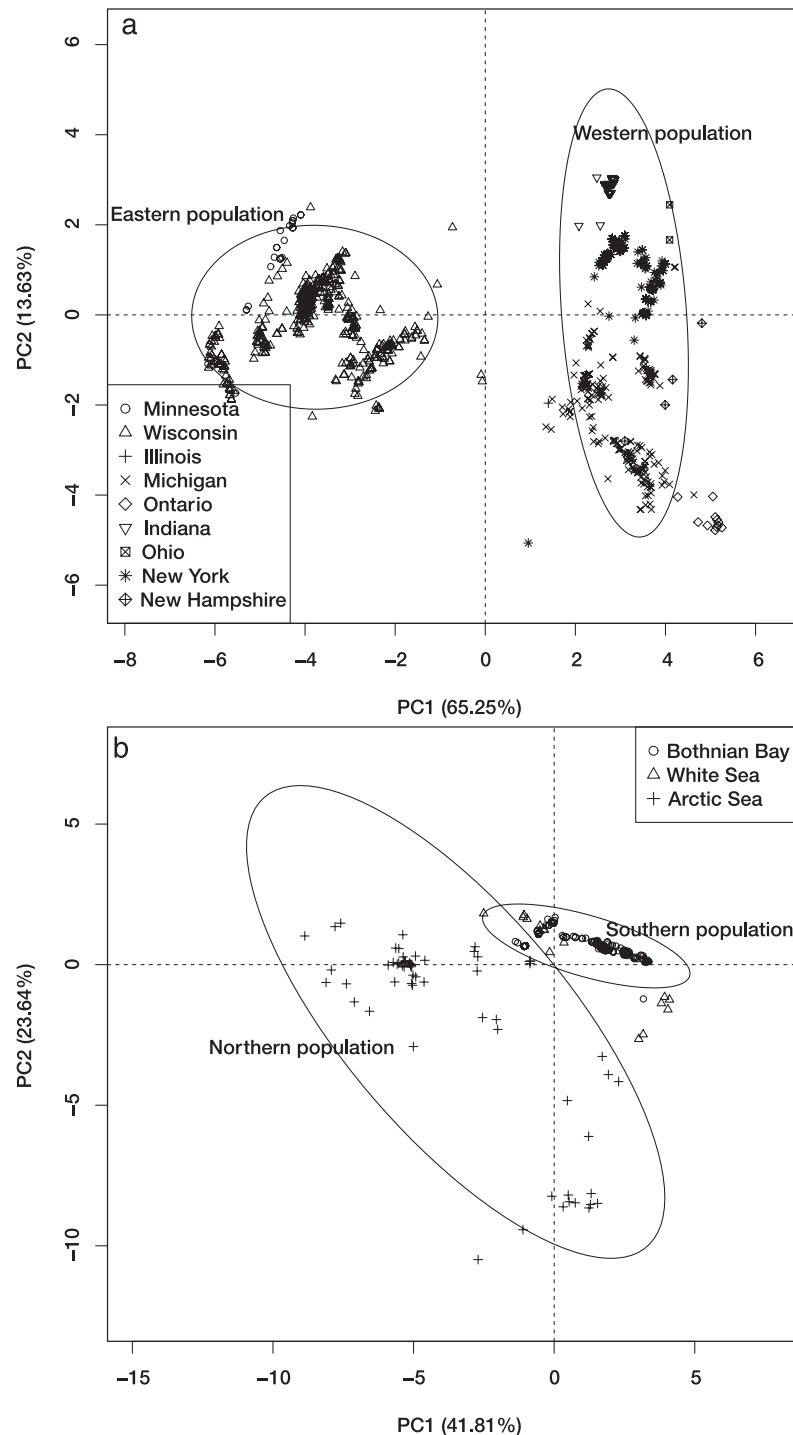


FIG. 2. PCA of the (a) KBB and (b) SP, using 19 bioclim variables. Circles represent 95% confidence intervals of population groupings. Percentages by axes indicate how much variation is explained by the principal components.

defined based on other PCA clustering patterns, delineating them into the two populations described here respects taxonomy and reflects how their geographical locations result in probable reproductive barriers (Kreivi et al. 2011).

Species distribution models

All mean testing AUC values for the models were higher than 0.95, which suggests that the model was able to distinguish between presence and background points

similar conditions relating to precipitation during the wettest time of the year.

In the PCA, precipitation of coldest quarter (PCQ), precipitation seasonality (PS), temperature of wettest quarter (TWeQ), mean diurnal range (MDR), and isothermality (IT) were important for distinguishing the SP populations. The modeled responses (Appendix S1: Fig. S4) of the populations differed for all of these variables, except for PS, for which responses between populations was similar. MDR, IT, TWeQ, and PS did not correlate strongly (>0.9) with any other variable. PCQ correlated strongly with several other variables that related to different aspects of precipitation (Appendix S1: Table S1). Therefore the populations might also experience different precipitation regimes in their current distribution.

DISCUSSION

Population-specific models describing climatically suitable areas for the populations of KBB and SP differed significantly from each other within a species and from the whole species model, suggesting that population-specific climatic conditions can be important in modeling species distributions. There was no overlap between the projected population models of the KBB and a slight overlap between the SP population projections. This may reflect the biology of the species, but it may also be an artifact of the modeling process caused by, for instance, different samples sizes and background points, complicated interactions between variables, or overfitting of the model. Investigating this is beyond the scope of this paper, but it could be studied using, e.g., sensitivity analysis, virtual species (LeRoy et al. 2015), or investigating the presence of non-analogue climates (Williams et al. 2007).

The PCA results indicated clearer environmental differences between the KBB populations than between the SP populations, which is reflected in the SDMs. Therefore, our population delineation may have affected the difference in overlap between the species. All SDMs predicted some degree of geographical shift in suitable sites as climate change proceeds; however, suitable area for KBB-East and SP-South would remain in close proximity to the current distribution until the late 21st century. The models for KBB-West and SP-South indicate loss of suitable conditions within their current distribution. However, if the study area covered a larger area further to the north, the SP-Whole model would likely identify more suitable locations. For the SP, expanding the study area northwards would probably have marginal effect because of the lack of terrestrial area to the north.

As would be expected from the PCA results, the niche similarity tests indicated that the populations of each species occupy different niches (Fig. 5). There are some changes in niche similarity over time, e.g., a substantial increase in all niche similarities of the SP by the 2040s. This may be caused by the suitable climatic conditions

left in northernmost Europe to which both SP populations are suited. Why climate is expected to change in this way, however, is beyond the scope of this paper. Generally, the climatic similarity in the inter-population model comparisons are consistently lower than the similarity indicated by any of the comparisons of population models to the whole species model. The main divergence can be seen for the comparison of the whole species model projection to that of the population model with fewer distribution points. The KBB-East and SP-North projections become less similar to the whole species projection with time, compared to the KBB-West and SP-South respectively. This indicates that the whole species models fail to represent climatically suitable areas for the populations and thus may not properly describe the future suitable areas for them. This emphasizes the need to study the basis of niche differences among populations, including local adaptation. The potential importance of such local adaptation can be explored with SDMs.

An important benefit of whole-species vs. population modeling is its power to guide experiments to detect functional differentiation and local adaptation. Specifically, the variable importances indicated by MaxEnt give some directions for identifying experimental variables in possible experiments on local adaptation between the populations. PCA also can be helpful in this regard, as it indicates what variables drive the differences between populations. MaxEnt (or other SDMs), however, has the added value of measuring variable importance for each population. If populations of KBB were functionally different in their two climatic niches, i.e., locally adapted, we predict that experiments manipulating seasonality, summer precipitation, and winter temperature would have the highest probability of yielding differences between populations. Experiments on local adaptation for the SP should concentrate on manipulation of conditions relating to temperature and changes in temperature during the day and year as well as conditions relating to precipitation regime over the year. Other parameters not included in this study may, however, also be important.

Implications for conservation

Failing to take population-level differences into account could lead to erroneous management decisions if populations are locally adapted. The populations of both case study species occupy different climatic environments according to the PCA, MaxEnt models, and niche similarity tests conducted in this study. If the populations have adapted to these differing conditions, intraspecific variation could be relevant when planning conservation of the species. Experimental studies are needed to disentangle this, but in lack of such information, readily applicable SDMs may offer one of the best tools to gain insight into the potential importance of niche divergence under climate change.

(KBB-Whole, 0.953 [SD = 0.006]; KBB-East, 0.977 [0.005]; KBB-West, 0.976 [0.002]; SP-Whole, 0.977 [0.011]; SP-South, 0.983 [0.02]; SP-North, 0.998 [0.006]).

Until mid-century, the predicted suitable area of both whole species models generally overlapped with that of the population-differentiated models, and the population projections coincided with different parts of the whole species prediction (projections for 2020s, 2050s, and 2080s in Figs. 3a and 4a; all time periods in Appendix S1: Fig. S2). After mid-century, this overlap continued to be prominent for the SP, while all KBB models predicted mostly different, i.e., non-overlapping, areas to be suitable (Figs. 3c and 4c). Across all time periods, KBB-West and KBB-East predictions never overlapped with each other (Fig. 3a), while SP-South and SP-North predictions overlapped minimally (Fig. 4a; 5.3% overlap in current climate, 12.6% in 2020s, 17.3% in 2030s, 22.0% in 2040s, 26.1% in 2050s, 20.8% in 2060s, 9.4% in 2070s, and 5.1% in 2080s). The number of projected suitable cells based on both SP population models were approximately equal to the predicted number of suitable cells of the SP-Whole (Fig. 4b), whereas the KBB population models together predicted fewer suitable cells than KBB-Whole (Fig. 3b). Towards the end of the century, the amount of suitable climatic area declined according to all models and disappeared from the study region altogether for KBB-West. The models also differed in their prediction of loss of current distribution area. KBB-East retained some of its current area while KBB-Whole and KBB-West lost all of its current distribution (Fig. 3c). SP-North lost suitability in all current areas while for the SP-Whole and SP-South some were retained, although the number of cells decreased during the century (Fig. 4c).

Niche similarity test

By using niche similarity tests, we compare how well the suitable climates of the modeled taxonomic units (populations or species) are represented by that of the other taxonomic units. Although the niches of the modeled units do not change, the degree to which they are represented in different time periods vary and this is captured by the test. Niche-similarity measures derived from the comparison of the modeled suitable area under current climate for the KBB and SP populations were low (KBB-West and KBB-East, $I = 0.1$; Fig. 5a; plot of D values in Appendix S1: Fig. S3b; SP-South and SP-North, $I = 0.09$; Fig. 5b). The similarity measurement of each of the two populations compared to the whole species was high, however (KBB-West vs. KBB-Whole, $I = 0.70$; KBB-East vs. KBB-Whole, $I = 0.68$; SP-North vs. SP-Whole, $I = 0.68$; SP-South vs. SP-Whole, $I = 0.71$).

We also measured similarity of projected suitability probabilities over time (Fig. 5; plot of D values in Appendix S1: Fig. S3). For the KBB, the values for the population vs. whole species comparison fluctuated over the century and by the 2080s, KBB-West was roughly as

similar to KBB-Whole ($I = 0.66$ in 2080s), as it was in the current projection ($I = 0.70$ in current). In contrast, KBB-East differentiated itself from KBB-Whole ($I = 0.56$ in 2080s). The two KBB populations' projected areas became more similar starting from mid-century (KBB-West vs. KBB-East in 2080s, $I = 0.19$). For the SP, all comparisons showed higher similarity by the 2040s (Fig. 5b). However, niche similarity, i.e., similarity in projected areas, for SP-Whole and SP-North decreased in the beginning of the century, increased during the 2040s, and ended up at the same level as in current climate in the 2080s (SP-North vs. SP-Whole in 2080s, $I = 0.65$; SP-South vs. SP-Whole, $I = 0.88$). In contrast, the SP-Whole vs. the SP-South comparison rose. The population comparison values stayed within the medium range; however, they obtained higher values at the end of the century than that they had in the beginning of the century (Fig. 5b; SP-South vs. SP-North in 2080s, $I = 0.38$).

Important variables

To understand what climatic conditions may be driving potential local adaptation and to inform possible future experiments of local adaptation, we identified the most important variables according to the models' permutation importance (Table 1) and PCA on VIF variables (Appendix S1: Table S2, Fig. S1). Response curves produced in the MaxEnt modeling process are in Appendix S1: Fig. S4. As the response curves represent how the predicted response changes for different values of the variable, while keeping all other climatic variables in the model at their average sample value, the response is context-specific and would change based on the set of covariates used in the same model. Also, as we did not include correlated variables, we cannot be sure that the omitted variables are not actually the ones governing the distribution of the species (Braunisch et al. 2013, Dormann et al. 2013). Therefore, we also discuss strongly correlated variables (>0.9 ; Appendix S1: Table S1) because they may differ between the populations in a similar way to the main variable.

Karner blue butterfly.—The most important variable (explaining $> 20\%$ of the model; Table 1) in the KBB-Whole model was temperature of the warmest quarter (TWaQ). All models of the KBB show a similar response curve for TWaQ (Appendix S1: Fig. S4), with a peak at around 20°C . TWaQ correlated strongly with annual mean temperature (AMT) and temperature of the warmest month (TWaM), of which the latter was removed prior to the modeling process. For KBB-West, precipitation seasonality (PS) was also important. The two population models showed the highest suitability within different ranges of PS, which suggested that the populations occupy separate climatic conditions regarding PS, with the KBB-West experiencing more seasonality in precipitation compared to KBB-East

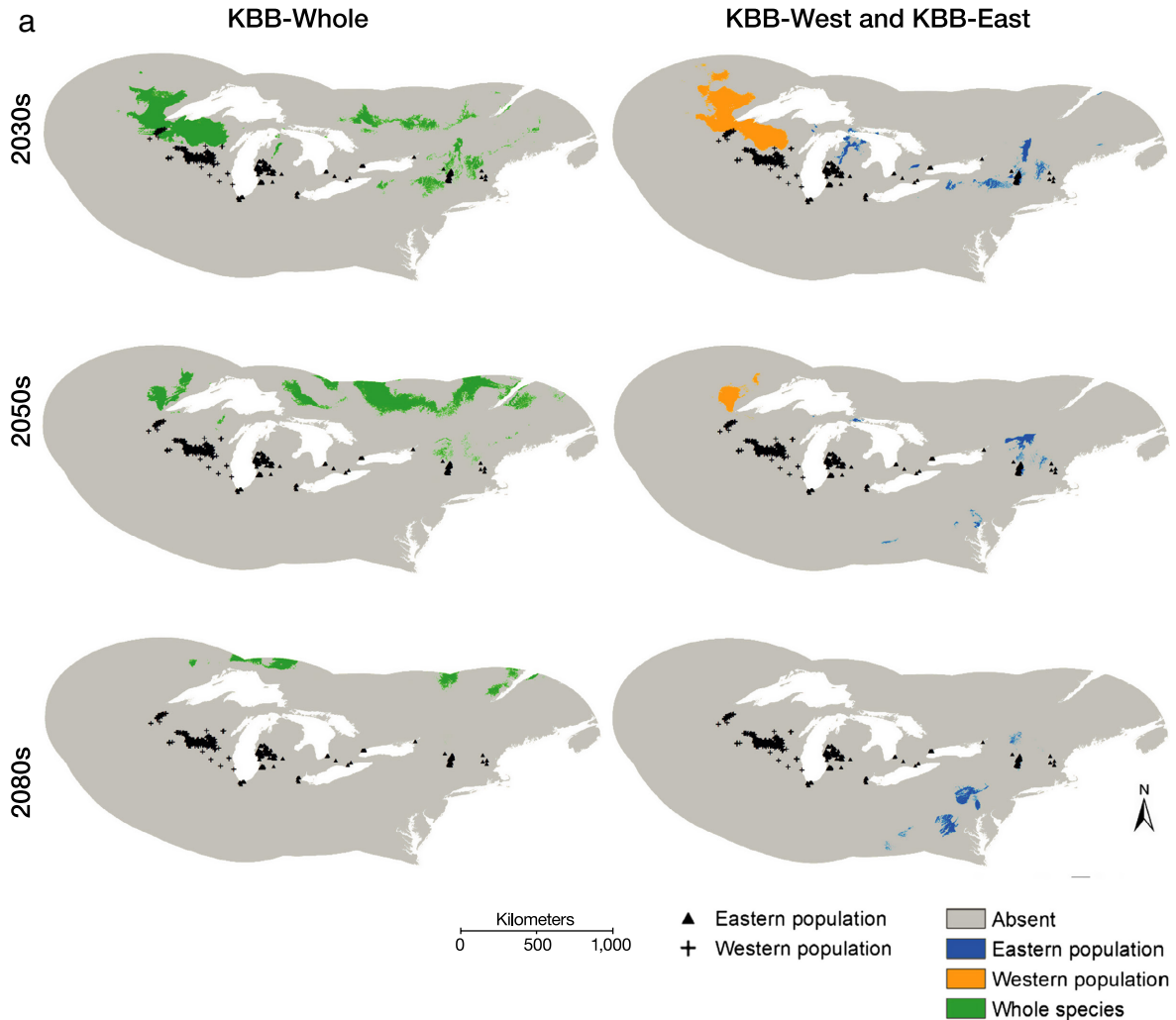


FIG. 3. KBB predictions. (a) Map shows predicted suitable distribution in 2020s, 2050s, and 2080s according to KBB-Whole (left column, projection in green) and KBB-West and KBB-East (right column, projections in orange and blue, respectively). (b) Change in predicted suitable grid cells for the KBB species and the two populations across time; populations combined is predicted suitable grid cells for KBB-West and KBB-East. (c) Spatial overlap with current distribution points (number of cells that overlap).

(Appendix S1: Fig. S4). However, strong negative correlations with precipitation of driest month (PDM), precipitation of driest quarter (PDQ), and precipitation of coldest quarter (PCQ) were noted. Precipitation during winter could therefore also differ for the populations.

In the PC analysis, temperature seasonality (TS), mean temperature of driest quarter (TDQ), and precipitation of warmest quarter (PWaQ) were important for distinguishing the populations of the KBB, and the modeled responses of the populations differed for these three variables (Appendix S1: Fig. S4). The populations experience different TS, with KBB-West experiencing more seasonality in temperature than KBB-East. TS correlated strongly with temperature of coldest month (TCM) and temperature annual range (TAR). Both relate to seasonality. TDQ and

PWaQ did not correlate strongly (>0.9) with other variables.

Siberian primrose.—The two most important variables in the SP models were mean temperature of driest quarter (TDQ; for SP-Whole and SP-North) and precipitation of warmest quarter (PWaQ; for SP-Whole and SP-South). The response of TDQ was similar for all the models (Appendix S1: Fig. S4). SP-South had a slightly broader positive response ranging from about -10°C to 10°C , however, while the response of the SP-North was high at values between approximately -8°C and 8°C . TDQ did not correlate strongly (>0.9) with any other variable, while PWaQ, the response of which is similar for all models, correlated strongly with precipitation of wettest month (PWeM). This can indicate that the populations experience

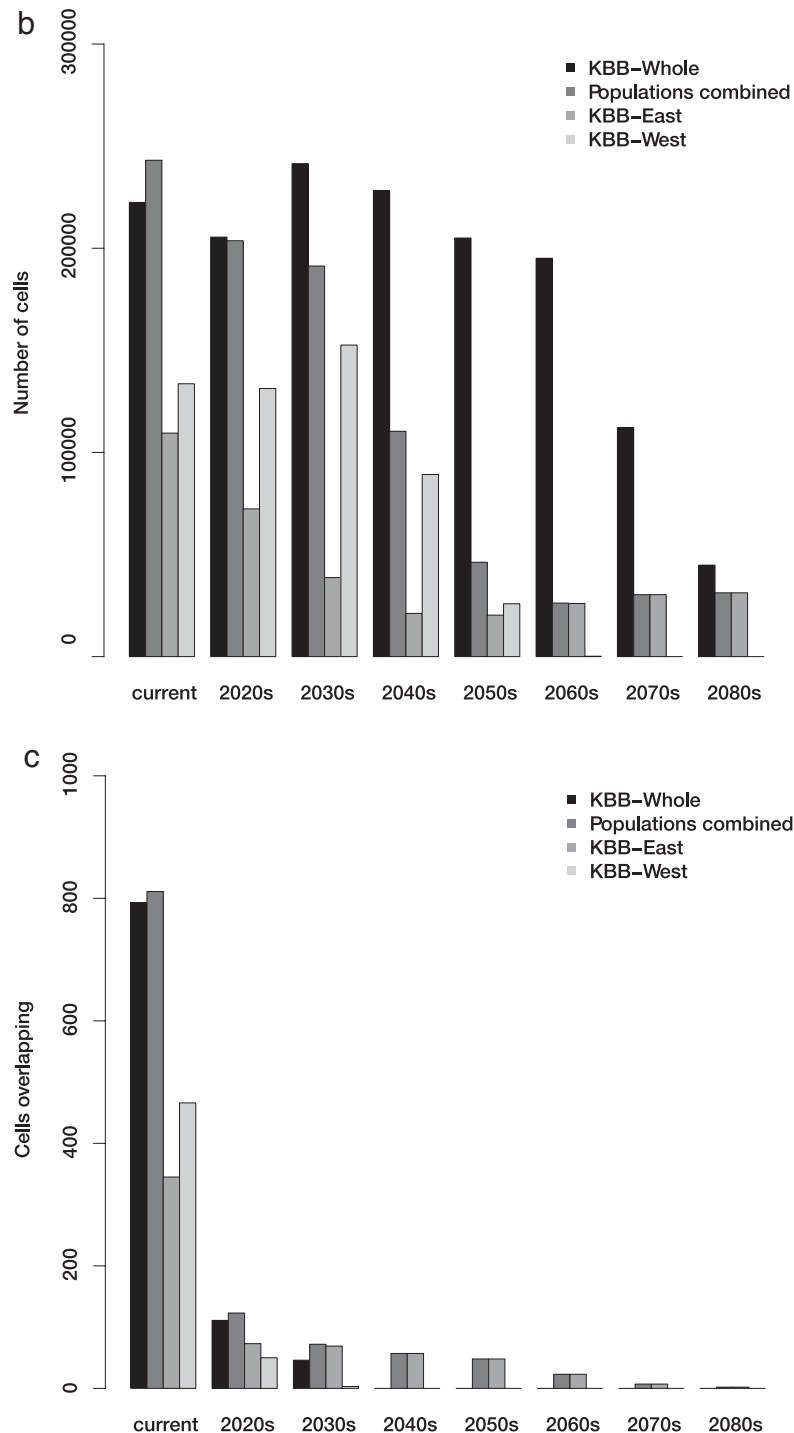


FIG. 3. (Continued)

To explore the conservation implications of either taking the possibility of local adaptation into account or ignoring it, we compare the risks of making a type I or type II error in this context (Fig. 6). When taking local adaptation into account in formulating SDMS with lack of experimental evidence, there are two opposing

assumptions that can be made: (1) the populations are locally adapted, or (2) there is no relevant local adaptation. Assumption (1) implies using population-based models and drawing up a corresponding conservation strategy A (Fig. 6), while assumption (2) leads the conservationist to use a whole species model and

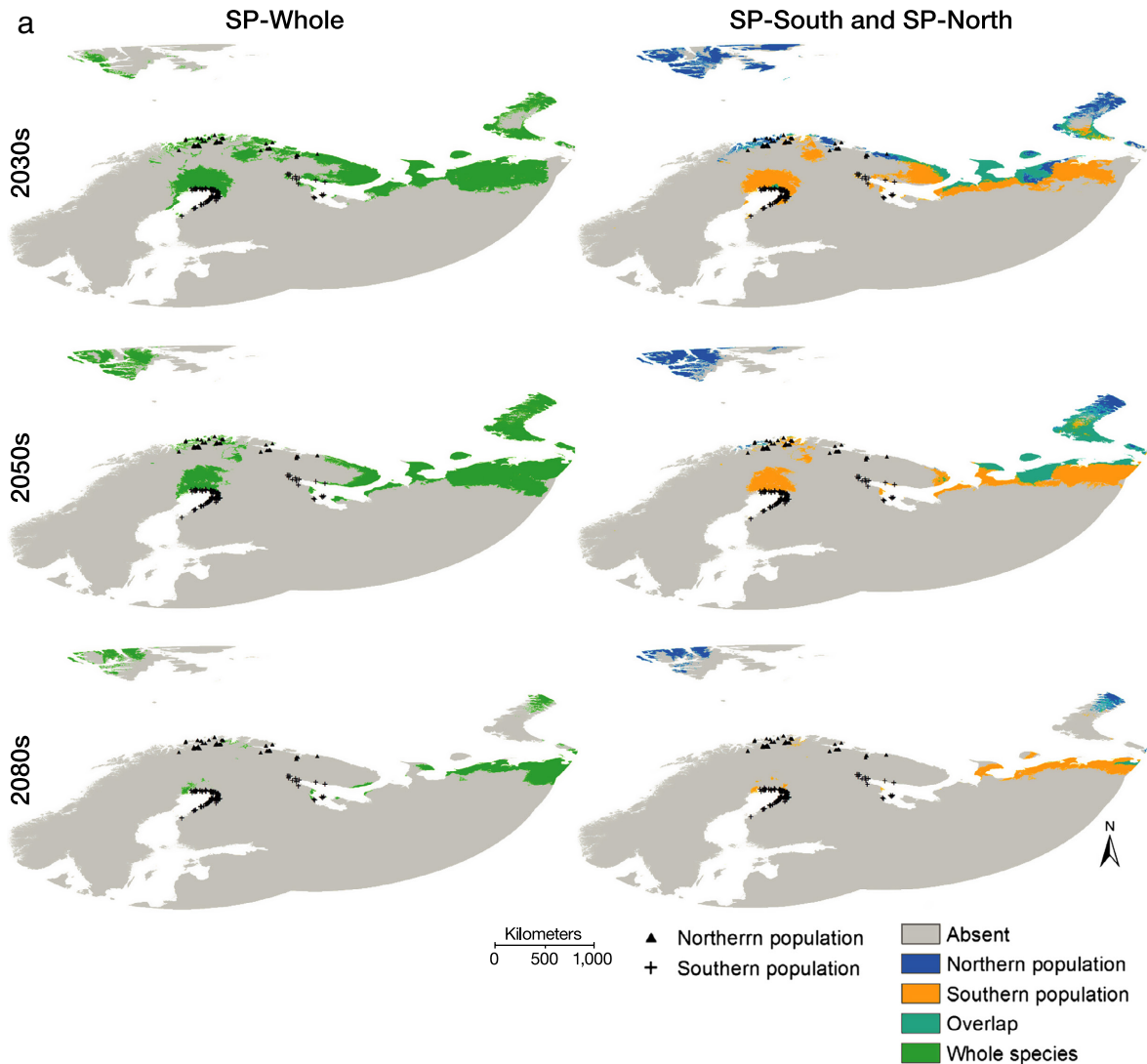


FIG. 4. SP predictions. (a) Map shows predicted suitable distribution in 2020s, 2050s, and 2080s according to SP-Whole (left column, projection in green) and SP-South and SP-North (right column, projections in orange and blue, respectively). (b) Change in predicted suitable grid cells for the SP species and the two populations across time; populations combined is predicted suitable grid cells for SP-North and SP-South. (c) Spatial overlap with current distribution points (number of cells that overlap).

conservation strategy B. Either assumption may be wrong, which would lead to us making a type I error (assuming local adaptation where there is none) or type II error (assuming no intraspecific differences when populations actually are locally adapted; Fig. 6). However, the two conservation strategies (A and B) can be more or less detrimental if they were the wrong choice.

For the KBB, implementation of a conservation strategy based on population models (assuming local adaptation; strategy A) could proceed by ex situ conservation (off-site, e.g., in a zoo) of KBB-West, as suitable climatic conditions for it disappear altogether, and assisted migration of KBB-East to new climatically suitable areas. If our assumption is wrong, and there is no substantial difference between the populations, we would

have made a type I error. In this case, we would have protected part of the species ex situ and assisted another part in its migration, however, not necessarily to the most favorable areas. The ex situ conserved individuals may still be used for reintroductions or assisted migrations. A conservation strategy based on the whole-species model (assuming no local adaptation; strategy B) could involve assisted migration to the new suitable areas in Canada. If this underlying assumption later turns out to be wrong, i.e., the populations turn out to be locally adapted, we have made a type II error. We would have assisted the species in its migration northward, but the locally adapted populations would have preferred conditions elsewhere, e.g., southwards in the case of KBB-East.

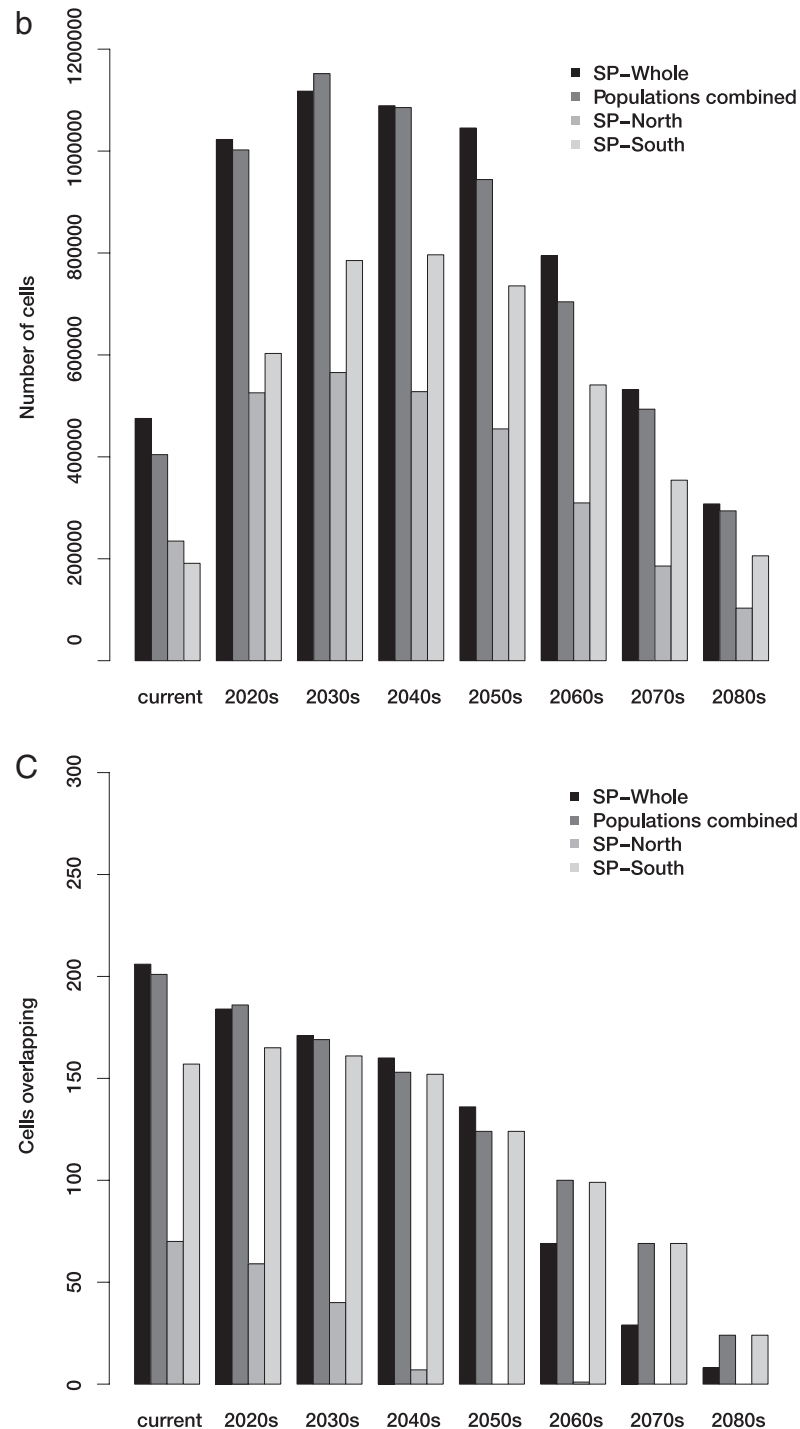


FIG. 4. (Continued)

For the SP, a population-based strategy could entail protecting SP-South in situ (on site; in its current location) for as long as possible and using assisted migration to move SP-South individuals to where SP-North currently occurs, as well as to other areas becoming climatically suitable in the northeastern part of the study

region. We could assist SP-North in its migration by moving representatives further north. If research later indicates that the populations are not locally adapted, this conservation strategy may still be beneficial since the whole-species model also indicates that the new receiving areas are suitable. We may, however, regret

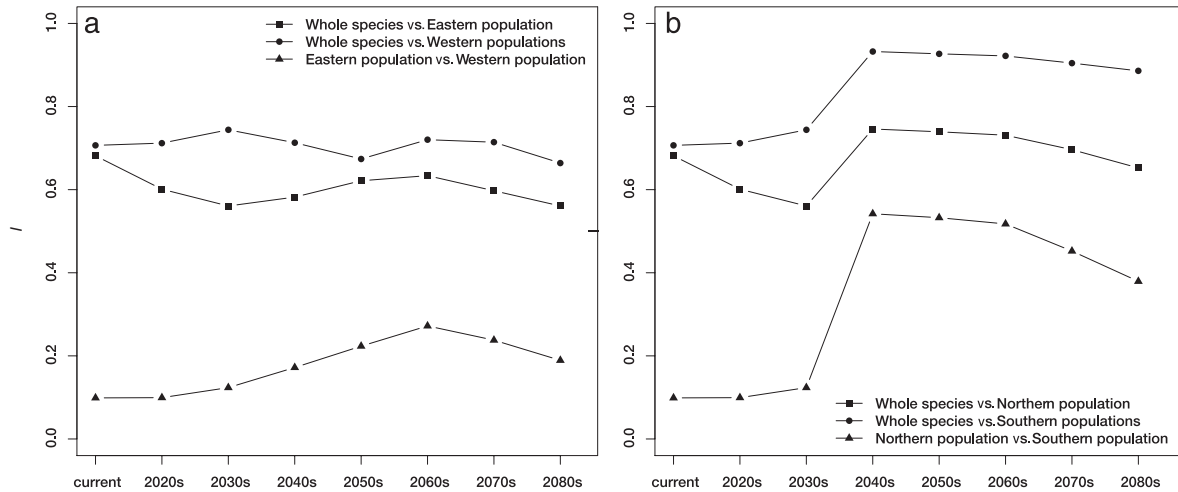


FIG. 5. I values, which are calculated from $1 - 1/2 \times$ Hellinger distance, based on the predicted suitability probabilities and predicted future climates for the (a) KBB and (b) SP models over time.

having assisted SP-South in its migration into the range of SP-North, since the northern population could have remained in the area, and we may have introduced pathogens or caused interbreeding of the populations, leading to loss of genetic diversity in other aspects than climatic adaptation. A whole species-based conservation strategy could consist of in situ conservation in all current areas and assisted migration of various representatives of the species to new suitable areas further north and towards the east. If we later discover that the populations are locally adapted, this conservation strategy may prove disadvantageous. Protecting

SP-South in situ would also have served the purpose in this case, but the current areas of the SP-North would not have remained suitable. Instead, it would have suited SP-South better. Depending on what source of individuals was used in the assisted migration project, the populations may have been introduced to incorrect areas.

One could argue that the local adaptation assumption and resultant conservation strategies are more cautious and the type I error (assuming local adaptation where there is none) therefore is less detrimental. This could be especially relevant for the SP, since the

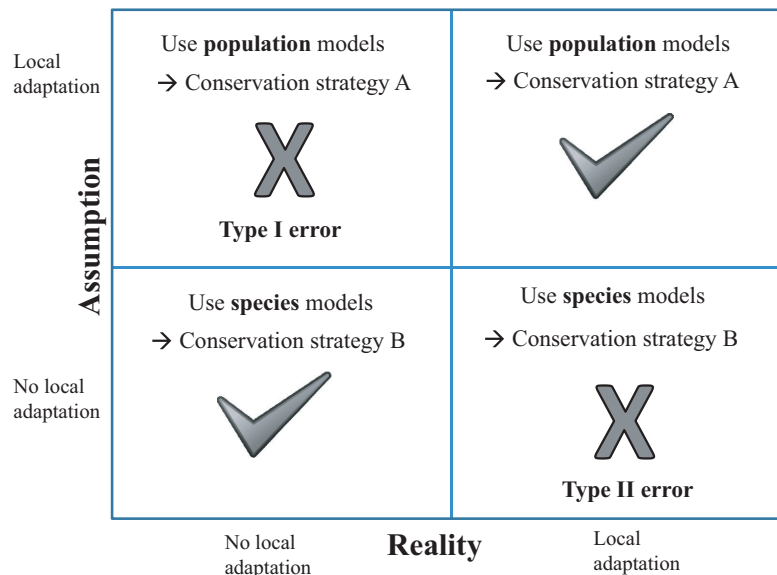


FIG. 6. Assumption vs. reality of local adaptation or undifferentiated populations. In cases where we do not know the degree of local adaptation, the effect on conservation of making a type I or type II error needs to be compared.

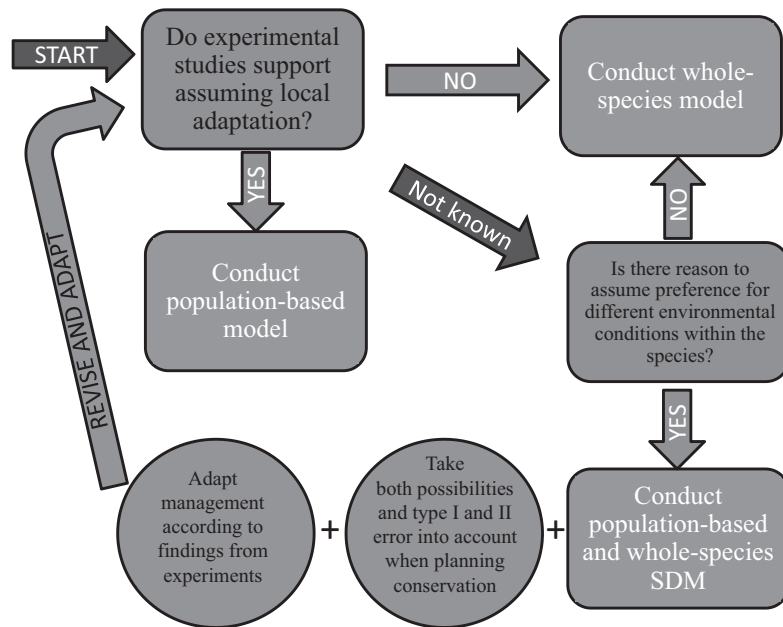


FIG. 7. Workflow for local adaptation consideration in conservation planning using SDMs.

population models distinguish different areas of the whole species model as suitable for the specific population, instead of pointing to additional ones. Nevertheless, if the risks involved with both errors are high and knowledge on local adaptation is lacking, combining aspects of both conservation strategies may be the best way forward until we have gained further information through experiments that can give a more mechanistic understanding of species responses to different environmental conditions (Morin and Thuiller 2009). For example, in the case of SP, such combined conservation efforts might include in situ conservation combined with assisted migration based on the whole-species model, through sourcing and distributing seed from SP locations that, based on the population models, most likely will be suitable for a specific receiving area. Opting for one main conservation strategy can be risky, and there may be more uncertainty involved in extinction predictions of SDMs than predictions of new suitable area (Schwartz 2012). Therefore, there is reason to be cautious with decisions involving discontinuing in situ conservation.

Workflow for considering local adaptation

To allow effective use of available SDM tools in conservation of species, managers could benefit from first-order approaches that can identify cases where the populations of a species may differ from each other and thus may need individual conservation attention, separate modeling, or diverse conservation strategies. We have identified important climatic parameters for designing experiments on local adaptation in two species and

illustrated how PCA and SDMs can be used to help guide experimental design for mechanistic experimentation that can aid in confirming the presence of local adaptation. Until such knowledge is obtained, however, SDMs continue to be useful tools for informing conservation. Nevertheless, SDMs should be used mainly as a first-order approximation and not as a direct and sole guide for decisions.

We suggest a workflow for situations where local adaptation between populations is likely but unknown (Fig. 7). The first step involves recognizing cases when local adaptation may require conservation attention. It is reasonable to assume that many species of conservation concern would possess varying degrees of adaptation to their local environments. Such cases include species with spatially distinct populations, reproductive isolation (Frankham et al. 2012), steep environmental gradients, species with taxonomic confusion (Kawecki and Ebert 2004), subspecies (Oney et al. 2013), or endangered species that are discontinuous across their range. If these species seem to inhabit separate climatic environments across their range, this may be an indication that they could be locally adapted. Until experiments, such as translocation trials, elucidate existence of local adaptation, we suggest modeling uncertain populations separately in addition to whole-species modeling. By comparing the effects of making a type I or type II error, risks can be taken into account and minimized. In many cases, incorporating aspects of both scenarios may be beneficial, especially when the risks are high. By applying cautious conservation and acknowledging the possibility of local adaptation, we can avoid losing biodiversity due to ill-advised decisions.

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LITERATURE CITED

- Abdi, H., and L. J. Williams. 2010. Principal component analysis. Wiley Interdisciplinary Reviews: Computational Statistics 2:433–459.
- Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends in Ecology and Evolution 22:42–47.
- Araújo, M. B., and A. T. Peterson. 2012. Uses and misuses of bioclimatic modeling. Ecology 93:1527–1539.
- Atkins, K. E., and J. M. J. Travis. 2010. Local adaptation and the evolution of species' ranges under climate change. Journal of Theoretical Biology 266:449–457.
- Austin, M. P., and K. P. van Niel. 2011. Improving species distribution models for climate change studies: variable selection and scale. Journal of Biogeography 38:1–8.
- Bakkenes, M., et al. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Global Change Biology 8:390–407.
- Banta, J., et al. 2012. Climate envelope modeling reveals intraspecific relationships among flowering phenology, niche breadth and potential range size in *Arabidopsis thaliana*. Ecology Letters 15:769–777.
- Benito Garzón, M., et al. 2011. Intra-specific variability and plasticity influence potential tree species distributions under climate change. Global Ecology and Biogeography 20:766–778.
- Bocedi, G., et al. 2013. Effects of local adaptation and interspecific competition on species' responses to climate change. Annals of the New York Academy of Sciences 1297:83–97.
- Bolnick, D. I., et al. 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist 161:1–2.
- Braunisch, V., et al. 2013. Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. Ecography 36:971–983.
- Craney, T. A., and J. G. Surles. 2002. Model-dependent variance inflation factor cutoff values. Quality Engineering 14:391–403.
- Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to quaternary climate change. Science 292:673–679.
- Dormann, C. F. 2007. Promising the future? Global change projections of species distributions. Basic and Applied Ecology 8:387–397.
- Dormann, C. F., et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.
- Early, R., and D. F. Sax. 2014. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. Global Ecology and Biogeography 23:1356–1365.
- Elith, J., et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.
- Elith, J., et al. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43–57.
- Fitzpatrick, M. C., and S. R. Keller. 2015. Ecological genomics meets community-level modeling of biodiversity: mapping the genomic landscape of current and future environmental adaptation. Ecology Letters 18:1–16.
- Forister, M. L., et al. 2010. After 60 years, an answer to the question: What is the Karner blue butterfly? Biology Letters 7:399–402.
- Fournier-Level, A., et al. 2011. A map of local adaptation in *Arabidopsis thaliana*. Science 334:86–89.
- Frankham, R., et al. 2012. Implications of different species concepts for conserving biodiversity. Biological Conservation 153:25–31.
- Franklin, J. 2010. Mapping species distributions. Spatial inference and prediction. Cambridge University Press, Cambridge, UK.
- Gompert, Z., et al. 2006. Identifying units for conservation using molecular systematics: the cautionary tale of the Karner blue butterfly. Molecular Ecology 15:1759–1768.
- Gompert, Z., et al. 2008. Recent colonization and radiation of North American *Lycæides* (*Plebejus*) inferred from mtDNA. Molecular Phylogenetics and Evolution 48:481–490.
- Grundel, R., et al. 1998. Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. Biological Conservation 85:47–53.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.
- Guisan, A., et al. 2013. Predicting species distributions for conservation decisions. Ecology Letters 16:1424–1435.
- Hällfors, M. H., et al. 2014. Coming to terms with the concept of moving species threatened by climate change: a systematic review of the terminology and definitions. PLoS ONE 9:e102979.
- Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. Global Ecology and Biogeography 13:469–471.
- Heikkinen, R. K., et al. 2006. Methods and uncertainties in bioclimatic envelope modeling under climate change. Progress in Physical Geography 30:751–777.
- Hijmans, R. J., et al. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.
- Homburg, K., et al. 2014. Evolutionarily significant units in a flightless ground beetle show different climate niches and high extinction risk due to climate change. Journal of Insect Conservation 18:781–790.
- Hultén, E., and M. Fries. 1986. Atlas of North European vascular plants: north of the Tropic of Cancer, vol. 1–3. Koeltz, Königstein, Germany.
- IPCC. 2007. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). R. K. Pachauri, and A. Reisinger, editors. IPCC, Geneva, Switzerland.
- IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on

- Climate Change (IPCC). R. K. Pachauri, and L. A. Meyer, editors. IPCC, Geneva, Switzerland.
- Jiménez-Valverde, A. 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modeling. *Global Ecology and Biogeography* 21:498–507.
- Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. *Ecology Letters* 7:1225–1241.
- Kreivi, M., et al. 2006. Isolation and characterisation of polymorphic microsatellite markers from *Primula nutans* (Primulaceae). *Molecular Ecology Notes* 6:334–336.
- Kreivi, M., et al. 2011. Regional and local spatial genetic structure of Siberian primrose populations in Northern Europe. *Conservation Genetics* 12:1551–1563.
- Kreyling, J., et al. 2014. Local adaptations to frost in marginal and central populations of the dominant forest tree *Fagus sylvatica* L. as affected by temperature and extreme drought in common garden experiments. *Ecology and Evolution* 4:594–605.
- Lampinen, R., et al. 2012. Kasviatlas 2011. Helsingin Yliopisto, Luonnontieteellinen keskusmuseo, Helsinki, Finland. [In Finnish.] Distribution maps <http://www.luomus.fi/kasviatlas>
- Le Quéré, C., et al. 2009. Trends in the sources and sinks of carbon dioxide. *Nature Geoscience* 2:831–836.
- Lê, S., et al. 2008. FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software* 25:1–18.
- Leroy, B., C. N. Meynard, C. Bellard, and F. Courchamp. 2015. virtualspecies, an R package to generate virtual species distributions. *Ecography* 38:1–9. doi:10.1111/ecog.01388
- Liu, C., et al. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28:385–393.
- Lobo, J. M., et al. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17:145–151.
- Mäkinen, L., and Y. Mäkinen. 1964. The distribution, ecology, morphology and taxonomy of *Primula nutans* Georgi ssp. *finmarchica* (Jacq.) Löve and Löve. *Annales Botanici Fennici* 4:273–291.
- McCormack, J. E., et al. 2010. Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation? Insights from tests with niche models. *Evolution* 64:1231–1244.
- McLachlan, J. S., et al. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* 21:297–302.
- Merow, C., et al. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36:1058–1069.
- Morin, X., and W. Thuiller. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90:1301–1313.
- Moruea-Holme, N., et al. 2010. Climate change risks and conservation implications for a threatened small-range mammal species. *PLoS ONE* 5:e10360.
- Nakicenovic, N., and R. Swart. 2000. Special report on emissions scenarios: a special report of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- O'Brien, R. M. 2007. A caution regarding rules of thumb for variance inflation factors. *Quality and Quantity* 41: 673–690.
- O'Neil, S., et al. 2014. Gene expression in closely related species mirrors local adaptation: consequences for responses to a warming world. *Molecular Ecology* 23:2686–2698.
- Oney, B., et al. 2013. Intraspecific variation buffers projected climate change impacts on *Pinus contorta*. *Ecology and Evolution* 3:437–449.
- Pearman, P. B., et al. 2010. Within-taxon niche structure: niche conservatism, divergence and predicted effects of climate change. *Ecography* 33:990–1003.
- Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361–371.
- Pelini, S. L., et al. 2009. Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. *Proceedings of the National Academy of Sciences USA* 106:11160–11165.
- Phillips, S. 2006. A brief tutorial on Maxent. AT&T Research, Middletown, New Jersey, USA. <http://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc>
- Phillips, S., et al. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modeling* 190:231–259.
- Ramirez, J., and A. Jarvis. 2008. High resolution statistically downscaled future climate surfaces. International Center for Tropical Agriculture (CIAT); CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS), Cali, Colombia.
- Rautiainen, P., et al. 2009. Management of three endangered plant species in dynamic Baltic seashore meadows. *Applied Vegetation Science* 10:25–32.
- Renwick, A. R., et al. 2011. Modeling changes in species' abundance in response to projected climate change. *Diversity and Distributions* 18:121–132.
- Romero, D., et al. 2013. Uncertainty in distribution forecasts caused by taxonomic ambiguity under climate change scenarios: a case study with two new species in mainland Spain. *Journal of Biogeography* 41:111–121.
- Schoener, T. W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704–726.
- Schwartz, M. W. 2012. Using niche models with climate projections to inform conservation management decisions. *Biological Conservation* 155:149–156.
- Stockwell, D. R., and A. T. Peterson. 2002. Effects of sample size on accuracy of species distribution models. *Ecological Modeling* 148:1–13.
- Synes, N. W., and P. E. Osborne. 2011. Choice of predictor variables as a source of uncertainty in continental-scale species distribution modeling under climate change. *Global Ecology and Biogeography* 20:904–914.
- Valladares, F., et al. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters* 17:1351–1364.
- Vergeer, P., and W. E. Kunin. 2013. Adaptation at range margins: common garden trials and the performance of *Arabidopsis lyrata* across its northwestern European range. *New Phytologist* 197:989–1001.
- Warren, D. L., et al. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62:2868–2883.
- Warren, D. L., et al. 2010. ENMTTools: a toolbox for comparative studies of environmental niche models. *Ecography* 1:607–611.
- Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences USA* 104:5738–5742.

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