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RESEARCH REVIEW

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Incorporating local adaptation into forecasts of species' distribution and abundance under climate change

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Abstract

Populations of many species are genetically adapted to local historical climate conditions. Yet most forecasts of species' distributions under climate change have ignored local adaptation (LA), which may paint a false picture of how species will respond across their geographic ranges. We review recent studies that have incorporated intraspecific variation, a potential proxy for LA, into distribution forecasts, assess their strengths and weaknesses, and make recommendations for how to improve forecasts in the face of LA. The three methods used so far (species distribution models, response functions, and mechanistic models) reflect a trade-off between data availability and the ability to rigorously demonstrate LA to climate. We identify key considerations for incorporating LA into distribution forecasts that are currently missing from many published studies, including testing the spatial scale and pattern of LA, the confounding effects of LA to nonclimatic or biotic drivers, and the need to incorporate empirically based dispersal or gene flow processes. We suggest approaches to better evaluate these aspects of LA and their effects on species-level forecasts. In particular, we highlight demographic and dynamic evolutionary models as promising approaches to better integrate LA into forecasts, and emphasize the importance of independent model validation. Finally, we urge closer examination of how LA will alter the responses of central vs. marginal populations to allow stronger generalizations about changes in distribution and abundance in the face of LA.

KEYWORDS

climate change, forecast, landscape demography, local adaptation, mechanistic distribution model, response function, species distribution model, transfer function

1 | INTRODUCTION

Predicting range shifts and population persistence in the face of climate change is a major ecological challenge, one that is further complicated by the potential for local adaptation (LA) to historical climate. Many species show strong reductions in performance when individuals are moved beyond range boundaries, suggesting that many distributional limits are driven by species' climate tolerances (Hargreaves, Samis, & Eckert, 2014; Lee-Yaw et al., 2016; Sexton & Dickman, 2016). But broad climate tolerances at the species level are generally comprised of narrower, locally adapted tolerances at the scale of populations (e.g., Angert, Sheth, & Paul, 2011; Hoffman, Anderson, & Hallas, 2002; Kelly, Sanford, & Grosberg, 2012; Sheth & Angert, 2014). Furthermore, such LA is common across both latitudinal and elevational ranges (e.g., Ågren & Schemske, 2012; Anderson, Perera, Chowdhury, & Mitchell-Olds, 2015; Angert & Schemske, 2005; Clausen, Keck, & Hiesey, 1940; Joshi et al., 2001). Taken together, these patterns provide strong evidence that climate tolerances vary throughout species' ranges (Bocedi et al., 2013; Fournier-Level et al., 2011; Jump & Peñuelas, 2005; King, McKeown, Smale, & Moore, 2017; Savolainen, Pyhäjärvi, & Knürr, 2007) and will influence responses to ongoing climate change, with local responses

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to climate change differing throughout a species' range (Gilman, Wethey, & Helmuth, 2006; Herrando-Pérez et al., 2018; Kelly et al., 2012; Pelini et al., 2009; Peterson, Doak, & Morris, 2018).

Unfortunately, most models that have been used to forecast species distributions under climate change assume that climate tolerances do not differ among populations (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp 2012). Failure to account for intraspecific variation in climate tolerances can introduce errors into forecasts about geographic distributions and the future viability of a species as a whole (Pearman, D'Amen, Graham, Thuiller, & Zimmermann, 2010), and precludes analysis of the fates of particular intraspecific lineages or the maintenance of genetic variation in ecologically important traits (D'Amen, Zimmermann, & Pearman, 2013; Marcer, Mendez-Vigo, Alonso-Blanco, & Pico, 2016). For example, if LA is strong, such that the breadth of environmental tolerances in local populations (including those at range edges) is much narrower than for a species as a whole (Holt, 2009), then locally adapted populations could be highly susceptible to climate change regardless of their position within the range, especially where the velocity of climate change (sensu Loarie et al., 2009) surpasses the species' dispersal ability and gene flow is limited by habitat fragmentation (Figure 1). Further, in the Northern hemisphere, warming has been and is predicted to be greatest at high latitudes (IPCC, 2014), raising the possibility that populations may be most vulnerable not at the southern range limit, where temperature is already warmer, but at the polar limit, where change will be faster (Figure 1). However, further complicating the picture is the possibility that, even with strong LA, polar-edge populations may, due to gene flow, perform better under conditions that are more benign than those they have historically experienced (Reich & Oleksyn, 2008; Yang, Pedlar, McKenney, & Weersink, 2015) and may also have broader climate tolerances due to historically greater climate variability (Deutsch et al., 2008; Janzen, 1967; Molina-Montenegro & Naya, 2012; Sunday, Bates, & Dulvy, 2011).

A particularly important consequence of including LA in range-shift forecasts is that it may overturn the commonly assumed "trailing-edge, leading-edge" range-shift pattern. Under this paradigm, species' distributions are expected to change primarily by expanding at the polar or cooler range edge, while contracting at the equatorial or warmer range edge where climate change will probably first exceed the species-wide upper thermal limit (Figure 1b, Maggini et al., 2011). Although this pattern has already been observed in many taxa, for many others it has not been seen, either in response to contemporary climate change (Chan, Hill, Ohlemüller, Roy, & Thomas, 2011; Groom, 2013; Moritz et al., 2008; Parmesan et al., 1999; Poloczanska et al., 2013) or during climate shifts in the past (Davis & Shaw, 2001; Hampe & Petit, 2005). In particular, the "trailing-edge, leading-edge" pattern of range shifts has occurred less consistently in terrestrial species than marine species (Sunday, Bates, & Dulvy, 2012). Although many mechanisms may interact with climate change to limit or alter range shifts (Anderson, Inouye, McKinney, Colautti, & Mitchell-Olds, 2012; Louthan, Doak, & Angert, 2015; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Suttle, Thomsen, & Power, 2007), several theoretical studies have highlighted the potential for LA to

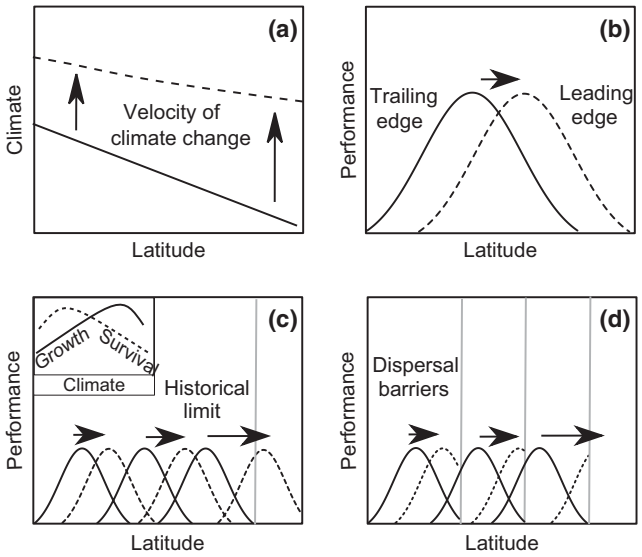


FIGURE 1 Changes in species distributions and abundances will depend on the magnitude of climate change, strength of local adaptation, and potential for dispersal. Shifts in both climate and species' performance from the present (solid lines) into the future (dashed lines) may differ across species' latitudinal ranges (or, equivalently, elevational ranges) in a variety of ways. (a) Climate is predicted to change throughout species' ranges but the magnitude of change may be greatest at high latitudes. (b) Without local adaptation, climate change is predicted to cause range contraction at the warm edge through declining performance (population growth or probability of occurrence) and expansion beyond the cold edge as species track their climate envelope. (c) Local adaptation to historical climate conditions will drive the redistribution of intraspecific lineages, with cold-edge populations moving beyond the historical range boundary and greater movement required where the velocity of climate change is faster (arrows). (Inset) The climate envelope of a particular population will depend on the responses of multiple vital rates, some of which may show opposing climate responses ("demographic compensation"). (d) Populations throughout the species' range may be at risk if there are barriers to dispersal, so that locally adapted lineages are unable to move to new areas with appropriate climate conditions

historical climate to drive nonintuitive patterns of range shifts. LA can result in range fragmentation, greater extinction risk, and loss of evolutionary diversity, including predominant losses of warm, cool, or even centrally adapted genotypes (Atkins & Travis, 2010; Bocedi et al., 2013; Valladares et al., 2014). The misperception that climate change effects will only manifest strongly at leading and trailing edges is also likely to curtail study of central populations, thus limiting our knowledge of range-wide climate change impacts.

While most recently published range-shift predictions have continued to ignore LA, an increasing number of studies are attempting to incorporate some form of intraspecific variation in climate responses. We note that genetically based variation in climate tolerances within species (hereafter "G × E," or gene by environment interactions) will influence responses to climate change whether or not it is consistent with a pattern of LA to historical climate and that few forecast studies distinguish between G x E in

general vs. LA in particular (see Results). Indeed, although climate tolerances may often be correlated with historical climate conditions throughout a species' range, the correlation is unlikely to be perfect due to gene flow, especially at range edges (Kirkpatrick & Barton, 1997; Paul, Sheth, & Angert, 2011). Given the growing recognition of the role that LA may play in shaping range shifts, more forecasts incorporating G × E are likely to soon appear, so now is a timely moment to assess the strengths and weaknesses of the approaches that have been adopted to date, to ask whether we can discern any generalities from these studies, and to identify best practices for including LA in future forecasts of climate responses.

In this review, we focus on approaches to incorporate existing G x E into forecasts of future climate responses. While the long-term biological impact of climate change will depend on future evolutionary processes, species' immediate responses to climate change will be shaped by current patterns of local adaptation to climate. This is particularly true for species with long generation times that may lack the capacity for rapid adaptation. Further, given the challenge of forecasting evolutionary dynamics (see Discussion), understanding the traits and environmental variables that have driven evolutionary adaptation in the past is a necessary first step to more speculative predictions of future evolutionary responses.

2 | REVIEW OF RECENT LITERATURE INCORPORATING INTRASPECIFIC VARIATION INTO RANGE FORECASTS

We searched ISI Web of Science on February 9, 2018, for studies that incorporated intraspecific variation into spatially explicit forecasts of species' distributions under projected climate (see Supporting Information Appendix S1). This yielded a total of 28 studies including 53 distribution models of 91 species (one model predicted 48 species simultaneously, Hamann & Aitken, 2013; and several studies made predictions for the same tree species). These included models for 32 plants (including 23 trees), 9 mammals, 4 birds, 2 reptiles, 1 amphibian, 4 insects, and 1 coral.

2.1 | Overview of differences among forecasting approaches

All of the studies included in our review (Table 1, Appendix S2) adopted one of three general methods to incorporate intraspecific variation into range predictions (see examples in Box 1). We now review the characteristics of the three methods and summarize the general strengths and limitations of each approach.

2.1.1 | Species distribution models

The most common approach, and also the simplest in terms of its data requirements, is to use a species distribution model (SDM, Franklin, 2009). SDMs represented 18 of 28 studies (64%) and 37 of 53 models in our review (Figure 2, Supporting Information Appendix S2). SDMs that incorporate intraspecific variation use known occurrences for each of two or more intraspecific groups, based on taxonomic, genetic, or biogeographic information, and the historical climate (and sometimes other abiotic and biotic variables) at those sites, and then project the distribution of all groups in the future climate. Modifications of the basic SDM approach use occurrences of community types that include a species to predict the frequency of that species across the future landscape (e.g., Gray, Gylander, Mbogga, Chen, & Hamann, 2011; Hamann & Aitken, 2013), or use data on survival of a species in multiple transplant gardens to fit a model that predicts probability of occurrence as a function of climate (Benito Garzón, Alía, Robson, & Zavala, 2011).

The prevalence of SDMs in general, and in analysis of intraspecific variation in species forecasts in particular, is directly related to the readily available data sources they employ and the ease of using well-developed software (e.g., MaxEnt; Phillips, Anderson, & Schapire, 2006). Other advantages of SDMs are that they commonly consider an extensive set of potential climate variables (Supporting Information Appendix S2), increasingly incorporate model uncertainty by using several algorithms, and build uncertainty in future climate into ensemble-based distribution forecasts (Table 1; Araújo & New, 2007; Thuiller, 2004).

Species distribution models, however, are agnostic about the underlying mechanisms shaping distribution and thus rely on the assumption that distributional patterns reflect differing climate tolerances of the intraspecific lineages. But intraspecific groups may occupy differing climate ranges by chance. Dividing a species' range into several groups is likely to yield different climate–occupancy relationships for each group even in the absence of LA. Conversely, many SDMs we reviewed rely on relatively coarse intraspecific groupings, such as subspecies or varieties (Figure 2a), which likely underestimate the true magnitude of LA to climate. Indeed, we could find no examples or arguments that show how SDMs by themselves can establish whether a species shows LA to climate. This makes it impossible to determine whether forecasts of whole-species SDMs or intraspecific SDMs are more likely to be correct without gathering additional information, thus weakening the advantage of their simple data requirements.

Very few of the SDM studies we reviewed looked for evidence of adaptation to local climate in the different intraspecific groups. However, a recent trend in SDM papers is to also use occurrence and climate data to test for similarity in the climatic niches of the groups (e.g., Hu et al., 2017; Ikeda et al., 2017, Meynard et al., 2017). An important caveat is that patterns of occurrence by themselves do not provide very strong tests of the hypothesis that intraspecific groups differ in their environmental tolerances. Tests for niche similarity (cf. Broennimann et al., 2012; Warren, Glor, & Turelli, 2008) typically compare the observed niche overlap between two groups (measured by statistics such as Schoener's D) to the distribution obtained by comparing occurrences of one group to randomized sets of pseudo-occurrences chosen repeatedly from within the range of the second group, thus accounting for differences in available environments

TABLE 1 Summary of the common practices, strengths, and weaknesses of methods used to incorporate intraspecific variation into species' distribution forecasts. Values are the number of models (out of the total number of models) of each method that include Model validation of (a) fitted lineage-specific climate response functions ("G × E"); (b) predicted distribution patterns ("distribution"); sources of uncertainty in forecasts due to (c) uncertainty in forecasted climate; (d) model structure or parameter values; (e) the geographic scale of variation in climate responses (including comparison to a species-wide model); and (f) present any evidence for intraspecific variation in climate responses relevant to the model ("evidence for G × E"), including from other experiments or previously published studies

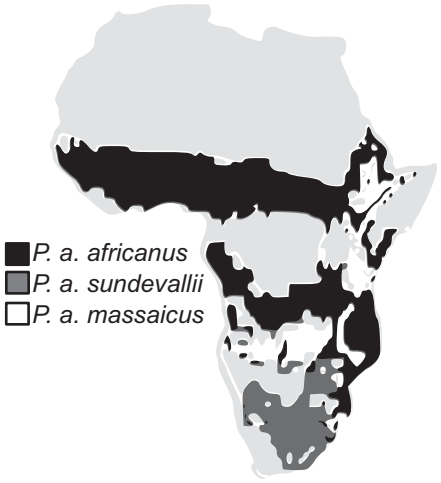
		Model validation		Sources of uncertainty in forecast						
Method	Data	G × E	Distribution	Climate forecast	Model/ parameter	Scale of G x E	Evidence for G × E	Strengths	Weaknesses	Example studies
SDMs	Current distribution and climate for few groups, often representing most of species range	0/37	34/37	16/37	8/37	25/37	8/37	Data and software availability, ensemble forecasts, extensive climate drivers	Correlative, assumes equilibrial distributions, cannot test for G × E	Marcer et al. (2016), Hällfors et al. (2016)
Mechanistic models	Variable quantity and resolution, experimental or correlative	1/8	8/8	0/8	1/8	1/8	2/8	Mechanism linking climate to performance	Limited vital rates, often strong assumptions	Buckley (2008), Chapman et al. (2017)
Response functions	Transplant performance, usually including many populations and environments	0/8	4/8	0/8	1/8	2/8	5/8	Climate responses predicted from climate of origin, applicable to new lineages.	Limited vital rates, data-intensive, extrapolation beyond garden environments	Wang et al. (2006), Oney et al. (2013)

between the two groups (followed by a parallel test in the other direction). While such tests can show whether intraspecific groups occupy more different environmental conditions than can be explained by background environmental differences between their two ranges, they do not unambiguously show that individuals of two groups would perform differently in the same environment. Many abiotic and biotic factors typically not examined in these tests could shape the environmental tolerances of a species. For example, geographic differences in the capacity of the substrate to hold moisture could mean that a plant species would only be able to persist at sites experiencing greater than average rainfall in one region, but could tolerate lower levels of

Box 1 Methods to forecast responses to climate change given intraspecific variation

Species distribution models

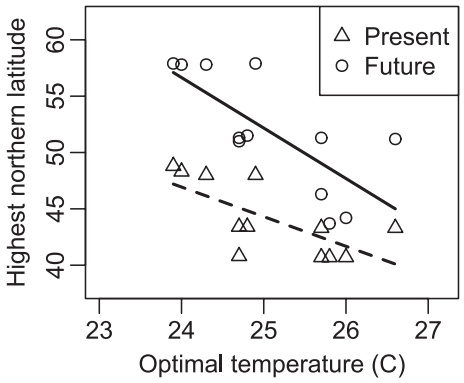
This approach infers the climate sensitivity of each intraspecific lineage based on the statistical relationship between its pattern of occurrence and one or more climate variables. For example, D'Amen et al. (2013) modeled the distributions of previously identified phylogeographic lineages within each of nine large mammal species in Africa. They used IUCN distribution maps to identify occurrences and absences for each phylogeographic lineage (between two and seven per species) and excluded lineages with very narrow distributions. They fit separate generalized boosted models (GBMs) to the presence/absence data for each lineage as well as species-wide models fit to all lineages and composite models representing the mean probability of occurrence of at least one lineage. Models were fit using six WorldClim bioclimate variables (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and cross-validated using 10% of the data in 10 random samples. The distribution of each lineage and species was forecasted for two future time periods and compared to the distribution of existing protected areas. They found that lineage-specific models predicted disparate climate responses within species and greater declines in suitable habitat relative to species-wide models.



Box Figure 1 Projected future distribution for warthog (*Phacochoerus africanus*) subspecies, modified from D'Amen et al. (2013).

Mechanistic models

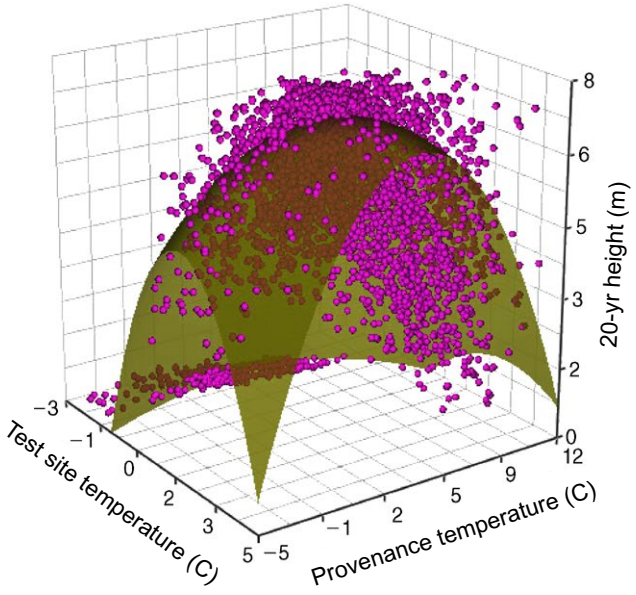
These approaches model the climate sensitivity of each intraspecific group by describing the mechanistic biological processes (e.g. phenology, physiology, or development) that link data on fitness or trait variation to climate responses in distribution or abundance. For example, Angert et al. (2011) quantified thermal performance curves (TPCs) for growth rate in 12 populations of the plant *Mimulus cardinalis* by experimentally manipulating growing temperatures. To relate TPCs to patterns of distribution, they used EcoCrop, a process-based model which estimates habitat suitability based on temperature and precipitation conditions relative to those needed for optimal growth. Separate temperature thresholds were inferred for each population from fitted TPCs while other parameters were assumed to be constant. They validated model predictions by comparison to independent occurrence data. The distribution under climate change was forecasted for each population separately, as well as species-wide models based on the average or range of fitted TPC parameters. How climate responses differed throughout the species range was then tested by relating the TPC parameters of each population to its local climate and range position. Angert et al. (2011) predicted that populations from higher latitudes and colder environments, which had lower thermal optima, and those with lower thermal breadth were at greater risk from climate change.



Box Figure 2 Populations' thermal optima affect predicted range shifts, modified from Angert et al. (2011).

Climate response functions

These approaches empirically measure the climate sensitivity of each intraspecific group using extensive transplant data to model performance as an interaction between source and site environmental conditions. For example, Wang, O'Neill, and Aitken (2010) used data on the 20-yr height of the tree *Pinus contorta* from 140 populations transplanted into 60 sites throughout British Columbia. They fit a multiple regression for height using population and test site temperature and heat: moisture variables and their interactions, as well as the geographic position of each site, as explanatory variables. The standard error of model predictions was computed by bootstrapping the dataset. Forecasts were generated for 1.6-km^2 grid cells in British Columbia by using the historical climate as population values and predicted climate as site values (i.e., assuming no dispersal) and also by using the population values that produced the highest forecasted growth (i.e., assuming optimal dispersal). Wang et al. (2010) predicted that climate change would have the most negative impacts in populations from historically warmer environments and in the warmest sites.



Box Figure 3 Performance as an interaction between source (provenance) and site mean annual temperature, modified from Wang et al. (2010).

precipitation in another. That is, the climatic niche of a uniform species could be influenced nonadditively by other factors that vary geographically, and this explanation for differences in the climatic conditions experienced by different groups in different areas would be difficult to distinguish from LA without data from reciprocal transplant or controlled climate experiments.

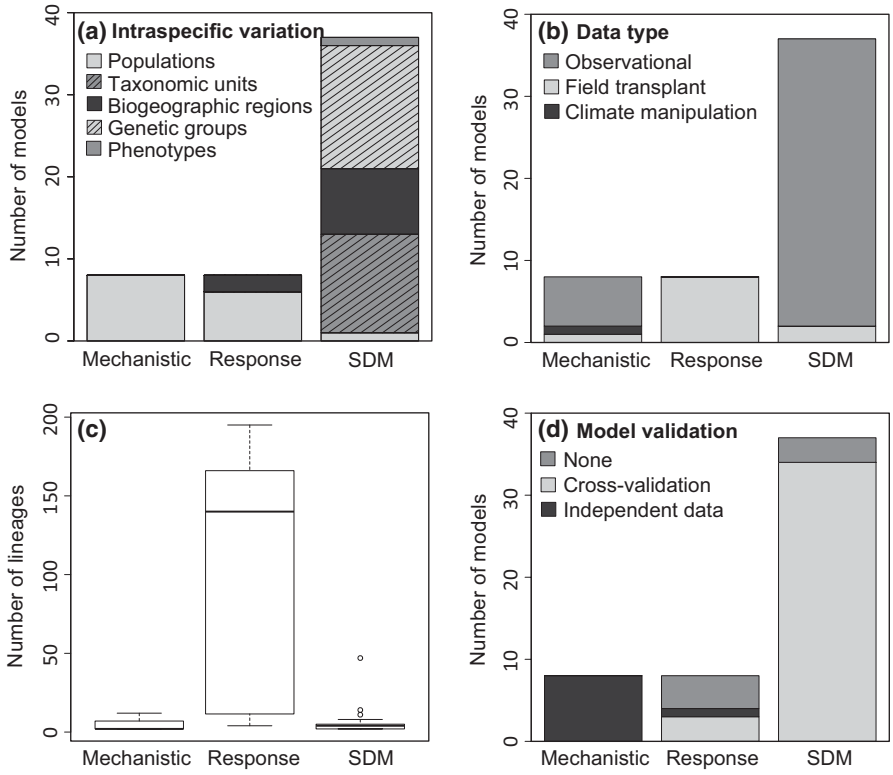


FIGURE 2 Summary of main approaches to incorporate intraspecific variation into published distribution forecasts. Barplots show the number of models of each method that used a particular approach. (a) Individuals within species were divided into groups with differing climate responses on the basis of populations, taxonomic units (e.g., subspecies, cultivars), biogeographic regions, genetic groups (e.g., haplotypes), or phenotypes. (b) Climate responses for each intraspecific lineage were estimated using observational data, field transplant experiments, or controlled climate manipulations. (c) The number of intraspecific lineages used in a given forecast model. (d) Forecast models were not validated, cross-validated using a portion of the dataset, or validated using an independent dataset

However, none of the SDM studies we reviewed used independent data to validate fitted models (Figure 2d). Further, we found only one SDM study that compared multiple approaches to delineating intraspecific groups (Marcer et al., 2016), even though different ways of grouping occurrences could lead to dramatically different forecasts.

2.1.2 | Mechanistic models

The second approach, which we are calling mechanistic models, uses information about the mechanism linking individual performance to climate, such as phenology, physiology, or climate-dependent development, to predict performance across space under future climate regimes. Mechanistic models require more knowledge about the biology of each species, tend to be more idiosyncratic between species relative to SDMs, and account for only four of the studies we reviewed (Appendix S2). Models used data ranging from variation in body size and prey availability in natural populations (Buckley, 2008) to flowering or leaf-out phenology in common gardens (Chapman, Scalone, Stefanic, & Bullock, 2017; Morin, Viner, & Chuine, 2008) to laboratory-estimated temperature-dependent growth curves (Angert et al., 2011). What unites these disparate approaches is that they combined data on intraspecific trait variation with mechanistic physiological, phenological, or developmental models to predict climate effects on distribution. The main advantage of this approach is that these models are developed from first principles and generally represent specific hypotheses about the mechanism linking climate to distribution. However, this strategy nearly always also requires strong assumptions for which little direct data are available. Perhaps for this reason, every study included an independent model validation step, by testing the ability of models to predict current distributions (Figure 2d). However, few evaluated the potential for different model structures or parameter values to substantively alter forecasts (Table 1).

2.1.3 | Climate response functions

These models use regressions of individual performance measures, such as growth or survival, from transplant gardens against climate variables at the site of the garden and also at the source location for each intraspecific group (i.e., "provenance"). The fitted regression ("response function" or "transfer function") is then used to predict future performance of all provenances across the landscape (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008). This approach requires extensive data and accounted for only 7 of the reviewed studies, all focused on commercially important tree species (Appendix S2).

The principal advantage of response function models is their ability to capture how the historical climate of a provenance shapes its responses to forecasted climate, which allows the response function to be applied broadly across the species' range (not only at transplant sites). Where data on multiple vital rates are available, this approach also allows forecasts for individual vital rates (e.g., separate forecasts for growth rate and survival, as in Valladares et al., 2014) as well as composite fitness metrics or occurrence. However, this is rarely done in practice as the goal of most provenance experiments and response function models has been to inform future planting recommendations for commercially valuable trees, and most forecasts have predicted tree productivity (measured in biomass per

hectare, or basal area) or height (Supporting Information Appendix S2). Moreover, none of the transplant studies has been carried out long enough to assess climate effects on recruitment, fecundity, or adult survival, even though the latter two are likely to strongly affect tree population growth (Caswell, 2001).

This method is also data-intensive, using on average 104 provenances and 34 gardens (range: 4–195 provenances, 4–62 gardens, Figure 2c), and, even so, frequently requires extrapolating fitted climate responses beyond the conditions observed in any experimental gardens to make forecasts (Wang, Hamann, Yanchuk, O'Neill, & Aitken, 2006). Although these studies have some of the best datasets with which to test for LA, few did so by comparing inferred climate optima or breadths to historical climate conditions across provenances (but see O'Neill, Hamann, & Wang, 2008; Wang et al., 2010; Yang et al., 2015). Finally, very few of the response function studies tested the ability of fitted climate functions to predict responses of other populations or gardens not used in the model fitting process, or evaluated the potential for different model structures or parameter uncertainty to substantively alter forecasts (Table 1, Figure 2d).

2.2 | Summary of past approaches

While the studies we found differ in many ways (Figure 2), some common issues emerge from our survey. We review these issues in this section, before turning to suggestions to address each of them in the following section.

First, while studies employing each method differ in the type and number of intraspecific lineages they considered, very few could clearly identify LA at the geographic scale being modeled (Table 1, Supporting Information Appendix S2). This is a critical consideration, as the spatial scale of LA to climate, relative to dispersal rates and the velocity of climate change, could have profound consequences for distribution forecasts. Instead, the type of intraspecific variation included in forecasts has primarily been determined by data availability and modeling approach rather than biological considerations; mechanistic models and response function studies primarily incorporated G × E at the level of populations, whereas SDMs recognized coarser intraspecific groups (Figure 2a).

Second, most studies used only observational data (Figure 2b) to assess differential responses to climate. Although observational datasets can be suggestive of LA effects, experiments that disentangle genetic and environmental effects on performance are necessary to rigorously test for LA to climate. All of the response function models used data from field common garden experiments, and in addition, they were the exception to the generally low replication used in data collection or analysis, including many more intraspecific lineages on average than either mechanistic models or SDMs (Figure 2c). However, of the 12 models that were parameterized using experimental data, only one used controlled climate manipulations (Angert et al., 2011) to unambiguously pinpoint climate adaptation, and no experimental study controlled for maternal effects, such as environmental effects on offspring quality (Mousseau & Fox, 1998), which can mask genetically based environmental responses (Kawecki & Ebert, 2004).

Third, although we found some effort at model validation, often these efforts did not assess the added uncertainty associated with incorporating LA into distribution forecasts. SDMs were the only models to incorporate uncertainty in future climate conditions when making forecasts, and were also more likely to compare intraspecific models to forecasts from a species-wide model (Table 1, Supporting Information Appendix S2), even though it would be straightforward to do both using other approaches. However, most models, especially SDMs, were cross-validated to a portion of the dataset (Figure 2d). Cross-validation cannot assess the ability of a model to accurately extrapolate to new lineages and environments, which necessarily occurs when forecasting responses across the species' range. Studies using mechanistic models were a notable exception; every mechanistic model was validated using an independent dataset on distribution or performance. This approach provides a rigorous test of the underlying climate-performance models, by evaluating their ability to predict the performance of new lineages under new environments as well as testing the relevance of specific performance metrics for determining distributions.

Finally, there were several other aspects of LA that were generally ignored in published studies that, while requiring additional data, could also have major impacts on species' responses to climate change. None of the studies we reviewed included climate responses across the entire life cycle of an organism or allowed climate tolerances to continue to evolve over time (Appendix S2). Only three studies considered LA to aspects of the local environment other than climate (Hu et al., 2017; Schwalm et al., 2016; Wang et al., 2010), and none considered LA to biotic drivers such as interacting species. Only two studies included empirical estimates of dispersal rates (Cacciapaglia & van Woesik, 2018; Morin et al., 2008) and none considered gene flow among intraspecific lineages or locations. We discuss each of these considerations, and their potential impact on species' forecasts, in greater detail below.

3 | IMPROVING FORECASTS OF CLIMATE CHANGE EFFECTS IN THE FACE OF LOCAL ADAPTATION

Having reviewed how recent papers have attempted to include intraspecific variation, ideally reflecting LA, into climate change forecasts, we now turn to approaches that could be used to improve such analyses. In our discussion, we start with steps that apply to current approaches and end with methods that either require new data or employ analytical methods that the recent papers did not utilize.

3.1 | Better addressing forecast uncertainty associated with local adaptation

In order for forecasts to be useful, they must accurately reflect the uncertainty inherent in any distribution model (Araújo & New, 2007). Incorporating LA into forecasts increases the complexity of distribution models (Figure 3), yet uncertainty in the strength,

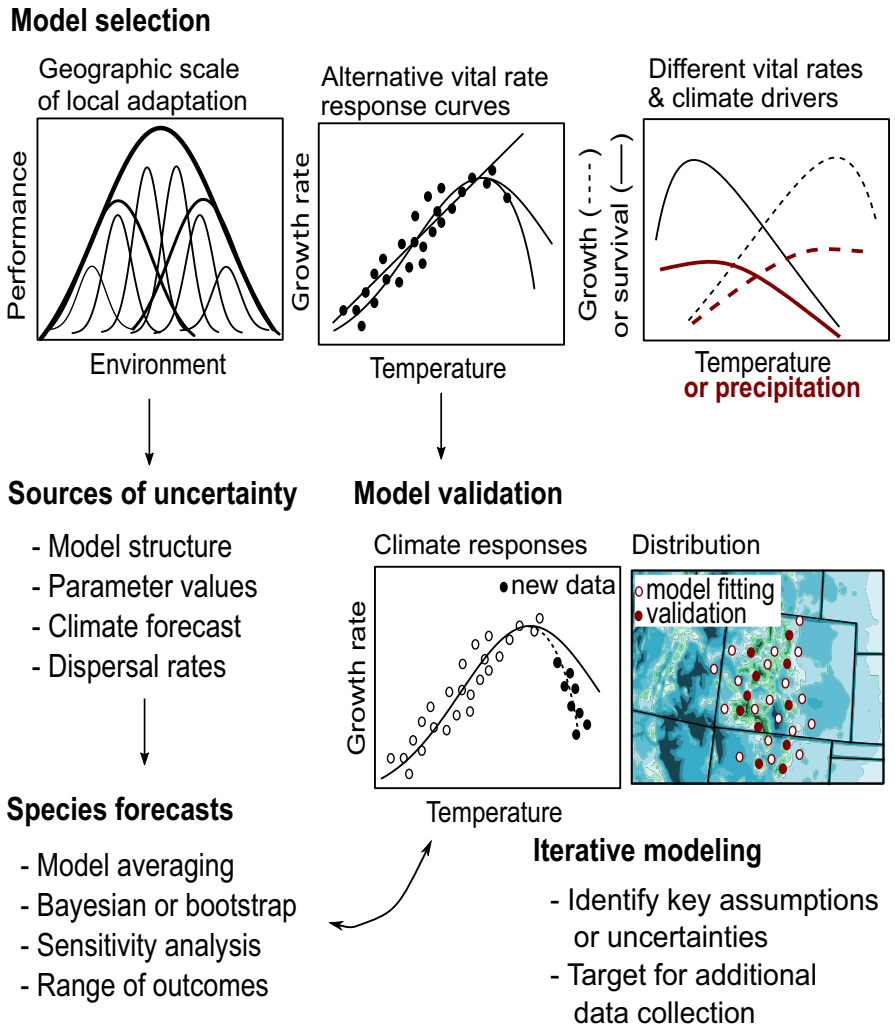


FIGURE 3 Steps to better account for uncertainty arising from local adaptation in species distribution forecasts. The process of building a distribution model should consider the potential for local climate adaptation to occur at different geographic scales, to follow different response curves, and to involve multiple vital rates and environmental drivers. Because of the uncertainty in model structure and parameter values, independent data should be used to validate fitted climate responses to new lineages or environments (open points and solid lines show original data and fitted Gaussian curve, solid points and dashed line show new data and updated asymmetric curve), as well as predicted distribution or abundance at new sites (open points show sites used to fit original model, and solid points show new sites used to validate predicted occurrence or abundance). Incorporating these sources of uncertainty into species forecasts will highlight targets for additional data collection, resulting in an iterative modeling–validation process to improve forecast precision

pattern, and geographic scale of LA has rarely been addressed. The spatial scale of local climate adaptation will differ within and among species depending on the steepness of environmental gradients, rates of gene flow, and the potential for phenotypic plasticity (Kawecki & Ebert, 2004; Richardson, Urban, Bolnick, & Skelly, 2014; Slatkin, 1987). Further, both performance and climate are highly multidimensional and locally adapted lineages will likely exhibit a range of responses across vital rates and environmental drivers (Figure 3). Climate responses are also frequently asymmetric, with sharp declines beyond some upper climate threshold (Angilletta, 2009; Deutsch et al., 2008; Martin & Huey, 2008). Alternative functional forms for modeling climate responses will, in particular, impact forecasts that extrapolate beyond the range of available data (Figure 3).

However, we found few examples of studies that carefully evaluated these sources of model and parameter uncertainty (Table 1), all of which arise when incorporating LA. Alternative models of LA, including different environmental drivers, intraspecific groupings, or functional forms for climate responses, could be integrated by averaging predictions weighted by AIC or some other measure of relative support (Akaike, 1974; Burnham & Anderson, 2004). For example, model-averaged forecasts could be used to reflect uncertainty in whether vital rates exhibit Gaussian vs. asymmetric responses to climate (Figure 3). Within a given model structure, uncertainty in the values of key parameters can be propagated into forecasts using Bayesian or bootstrapping approaches (Merow et al., 2014; Wang et al., 2010) or quantified with sensitivity analysis (Buckley, 2008). Finally, establishing a range of forecast outcomes can be an effective tool to understand the sensitivity of predictions to assumptions for which few data are available, such as comparing models with or without LA (e.g., Angert et al., 2011; Pearman et al., 2010).

Increasingly, researchers have recognized that species' forecasts should convey uncertainty (Buisson, Thuiller, Casajus, Lek, & Grenouillet, 2010; Guisan et al., 2006; Hartley, Harris, & Lester, 2006), but this needs to include the uncertainty associated with the pattern, strength, and geographic scale of LA. In particular, we have little understanding of how LA compares to the effects of other, well-known sources of uncertainty in distribution forecasts, such as different modeling algorithms, climate forecasts, or dispersal scenarios (Buisson et al., 2010; Engler et al., 2009).

Given these multiple sources of uncertainty in fitting models that include LA, collection of independent data that can be used to validate model predictions should be a high priority, to quantify both the accuracy of fitted climate responses and their ability

to capture patterns of distribution (Figure 3). This can include laboratory or field experiments that test predicted responses to forecasted climate or the collection of data from new populations not used in the fitting process. In addition to validating climate responses, the ability of a model to capture current distributions can be evaluated by sampling new locations throughout the species range and assessing the ability of the model to predict presence of the species at those locations ("present-casting"); these same steps can also be applied to demographic rates or abundances. This step is especially important for understanding the ability of models to interpolate LA to new populations and environments. Independent model validation is a powerful tool, enabling an iterative modeling process whereby key sources of forecast uncertainty can be identified and targeted for additional data collection (Figure 3).

3.2 | Interpolating climate responses throughout species' ranges

An important and outstanding challenge for distribution models is how to apply local climate sensitivities, often estimated for a narrow subset of lineages, field sites, or environments, to predict future performance throughout the species range. For example, several studies have developed detailed models of varying climate responses along environmental gradients, but stop short of forecasting changes in species' distribution (Crozier, Zabel, & Hamlet, 2008; Kingsolver & Buckley, 2018). Perhaps the most biologically realistic approach would be to use historical environmental conditions to infer a population's likely response to future climate. Field and laboratory experiments suggest that many populations perform best under conditions that are similar to their historical climate (Eliason et al., 2011; Hoffman et al., 2002; Wilczek, Cooper, Korves, & Schmitt, 2014). The exceptions are populations from high latitudes or elevations, which often perform better under conditions that are more benign than they have typically experienced (i.e., "countergradient variation"; Conover & Present, 1990; Fangue, Podrabsky, Crawshaw, & Schulte, 2009; Reich & Oleksyn, 2008). However, the positive effects of warming in these portions of the range may only occur with a very limited amount of warming and could also be mitigated by biotic effects such as competition that may also increase with warming (e.g., Alexander, Diez, & Levine, 2015; Compagnoni & Adler 2014; Klanderud & Totland 2007). This suggests that tying peak performance to average local climate and incorporating geographic trends in the breadth of climate/performance relationships could be the best way to interpolate climate responses from well-studied populations to new sites throughout the species range. Response function studies come closest to this goal, predicting performance at any site based on historical and future climate. However, populations from similar climates can also show significant variation in their responses to climate change (Wang et al., 2006), and this variation has so far not been propagated into any forecasts. Indeed, most studies we reviewed did not attempt to interpolate patterns of LA, but instead aggregated separate forecasts across lineages to predict the species-level distribution under climate change (D'Amen et al., 2013; Pearman et al., 2010). This approach is most plausible when the chosen intraspecific lineages are representative of the entire species and the geographic scale of LA is broad, but these assumptions need to be justified.

The potential for adaptation to aspects of the local environment other than climate will further complicate interpolation across the species range. For example, most distribution models use climate drivers such as temperature or precipitation regardless of whether this variation occurs across altitudinal or latitudinal gradients, which may differ in other variables that modulate climate responses. For example, competition with newly co-occurring species, changes in photoperiod, or other nonclimate abiotic factors such as soils could limit the ability of lineages to expand their ranges into otherwise climatically suitable habitat (Griffith & Watson, 2006; Merrill et al., 2008). The extent to which climate responses across altitude are predictive of climate responses across latitude, or vice versa, remains a major outstanding question (De Frenne et al., 2013; Jump, Matyas, & Peñuelas, 2009; Matias & Jump, 2015). Wang et al. (2010) considered interactions of climate variables with latitude, longitude, and elevation to allow for geographically constrained climate responses; support for inclusion of these indirect variables suggests the importance of other, correlated aspects of the environment (Austin, 2002). Only three studies in our review considered LA to nonclimate environmental drivers, all of which were abiotic variables such as soil type or topography that were assumed to remain static over time. No study attempted to include LA to biotic drivers, such as interacting species, that could also shift under climate change. Intraspecific variation can have profound impacts on species interactions (Des Roches et al., 2018; Moran, Hartig, & Bell, 2016), suggesting LA to biotic drivers is an important consideration in applying climate responses across the species' range and should be a high priority for independent model validation.

3.3 | Estimation and use of empirical dispersal and gene flow rates

Whether species will be able to disperse sufficiently quickly to track shifting climate conditions has profound consequences for forecasts of species distribution under climate change (Engler et al., 2009; Schloss, Nuñez, & Lawler, 2012). Incorporating LA only magnifies the importance of dispersal, as it will determine the redistribution of intraspecific lineages throughout the species range, with important consequences for the conservation of genetic variation (Sgro, Lowe, & Hoffmann, 2011). For example, several studies have paired traditional species-wide SDMs, which do not incorporate LA in responses to climate, with range-wide genetic sampling to infer the loss of unique genetic lineages in the warmer portions of the species range due to predicted declines in habitat suitability there (Bálint et al., 2011; Buonomo et al., 2018; Neiva et al., 2015). However, other studies directly incorporating LA into distribution models have predicted warmer-adapted lineages to expand their distributions under climate change (Benito Garzón et al., 2011; Kapeller, Lexer, Geburek,

Hiebl, & Schueler, 2012). In general, if populations are strongly adapted to local climate conditions, then in situ persistence under climate change could be low throughout the species range (see Figure 2 in Peterson et al., 2018). In this case, the relative risk to different lineages will depend critically on rates of dispersal. If dispersal rates are high, then warmer-adapted lineages may be able to persist by replacing colder-adapted lineages, whereas colder-adapted lineages may have to disperse well beyond the historical range and could therefore be at greater risk, particularly for polar or alpine species (Figure 1).

Although most distribution forecasts that incorporate LA assume either unlimited dispersal or compare unlimited and no dispersal scenarios, potential dispersal rates for intraspecific lineages will likely have fairly narrow bounds. To better characterize dispersal, some studies have used direct estimates of dispersal rates (Cacciapaglia & van Woesik, 2018; Morin et al., 2008), whereas others have assumed dispersal will be constrained by land use boundaries (D'Amen et al., 2013; Hamann & Aitken, 2013; Schwalm et al., 2016). More complex models could incorporate spatially varying dispersal rates due to habitat fragmentation or biotic filters, or even the potential for dispersal traits to evolve at shifting range margins (Phillips, Brown, Webb, & Shine, 2006; Williams, Kendall, & Levine, 2016). Placing biologically grounded bounds on dispersal rates will improve our ability to predict the redistribution and potential loss of genetic lineages and ecologically important traits. Achieving this goal would be facilitated by additional computational tools, such as MIGCLIM (Engler, Hordijk, & Guisan, 2012) or RangeShifter (Bocedi et al., 2014), that can incorporate dispersal into grid-based distribution models (Chipperfield, Holland, Dytham, Thomas, & Hovestadt, 2011). Although many species-wide forecasts have emphasized greater risk in the warmest portions of species ranges, identifying the areas of greatest conservation concern may depend on whether the focus is on preserving specific lineages (perhaps as a means to ensure adaptability to future conditions range-wide) or simply maintaining healthy populations, regardless of their genetic composition, within a particular geographic region (Bálint et al., 2011; Crandall, Bininda-Emonds, Mace, & Wayne, 2000; D'Amen et al., 2013; Sgro et al., 2011).

Finally, as intraspecific lineages shift their distributions under climate change, a critical question is how gene flow among divergently adapted lineages could alter climate responses. In all of the studies we reviewed, climate sensitivities were assumed to remain static into the future. Yet there is a growing effort to incorporate ongoing evolutionary dynamics into models of climate change responses (Bocedi et al., 2014; Bush et al., 2016; Cotto et al., 2017; Kearney, Porter, Williams, Ritchie, & Hoffmann, 2009; Thuiller et al., 2013). For example, AdaptR (Bush et al., 2016) allows thermal response curves of Drosophilids to evolve under changing climate conditions. To our knowledge, none of these approaches have yet incorporated intraspecific variation in initial climate responses to account for LA to historical climate conditions. However, this would be straightforward to implement if the data were available (Bush et al., 2016). LA could also be simulated for historical climate conditions and then compared to current patterns of intraspecific variation to validate their use in forecasting future evolutionary change. Dynamic evolutionary models require information on individual variation in responses to climate within populations, such as the heritability of thermal optima or breadth. Collecting these data for multiple populations to incorporate LA requires experimentally tractable organisms and thus will be even more difficult than current approaches that account for the short-term effects of LA but ignore the potential for future evolutionary change. However, where feasible, dynamic evolutionary models that account for LA to historical climate conditions could be used to explicitly test differing hypotheses about the joint effects of dispersal, gene flow, and evolutionary potential in driving species' responses to climate change.

3.4 | Taking advantage of existing local adaptation datasets to improve forecasts

The majority of studies we reviewed relied on occurrence data, from which inference about LA is extremely constrained (see above). However, datasets on local climate adaptation are abundant (Bocedi et al., 2013; Fournier-Level et al., 2011; Jump & Peñuelas, 2005; King et al., 2017; Savolainen et al., 2007). Nonetheless, linking LA datasets to models that can predict species-wide patterns of distribution or abundance will be challenging. Perhaps the most obvious issue is the replication of environmental conditions and populations necessary to parameterize a species-wide distribution model. Among the studies we reviewed, those based on experimental data used an average of 1,050 (median = 134, range = 9–3,600) population × environment combinations.[1] In contrast, a review of reciprocal transplant experiments found an average of 11.2 (median = 4, range = 2–72) population–garden combinations[2] (Hereford, 2009). However, it may be the case that capturing responses at environmental extremes, as is common in transplant experiments, is more important than high levels of replication to accurately parameterize distribution models with LA. Wang et al. (2010) performed a rarefaction analysis for a response function model and found that model precision was not greatly increased beyond 49 populations and 21 test sites, or about 12% of the dataset used to parameterize the full model. However, it would be useful to expand this approach to additional datasets and to test the effects of capturing populations and gardens representative of environmental extremes relative to random subsampling.

Datasets that span multiple years also increase the power to observe limiting conditions and detect locally adapted climate responses. The studies we reviewed all used time-averaged measures of climate and performance, such as 30-year climate summary statistics (WorldClim bioclimatic variables; Hijmans et al., 2005), historical occurrences, or diameter at breast height after 20 years (Wang

[1] We were only able to estimate the number of combinations for 10 of 12 models with experimental data, some of which used the same dataset in multiple studies (Appendix S2).

[2] We calculated the number of combinations used in each study in the Appendix of Hereford (2009).

et al., 2006). However, demographic studies have shown that rare bad years can profoundly limit population growth and persistence (Boyce, Haridas, Lee, & The Nceas Stochastic Demography Working Group, 2006; Lewontin & Cohen, 1969; Tuljapurkar & Orzack, 1980; Young, 1994), suggesting that time-averaged climate and performance measures are both oversimplified and less powerful for detecting LA than are annual data. Careful analyses of the sensitivity of model predictions to levels of replication, including over time, would shed light on the potential to use sparser, but more readily available, experimental or demographic data sets, while also establishing guidelines for the design of future studies. Sparser LA datasets can also be used in combination with more readily available presence/absence or abundance data to infer distribution, using hidden process or inverse modeling approaches (reviewed by Evans, Merow, Record, McMahon, & Enquist, 2016).

3.5 | Taking demographic approaches to forecasting distribution and abundance

Importantly, no study in our review addressed how the population growth rate, perhaps the ultimate determinant of distribution (Birch, 1953; Pulliam, 2000), will respond to climate change given LA, although Buckley (2008) predicted patterns of abundance that several populations might achieve across the range. Instead, existing studies have mostly predicted occurrence, whereas forecasts of local abundance would be far more useful for predicting the ecological and conservation impacts of climate change (Cotto et al., 2017; Ehrlén & Morris, 2015). That said, it is not trivial to determine how LA will impact climate responses in the full set of vital rates that determine population growth rate, abundance, and the likelihood of persistence. Existing approaches, based on data for one or a few vital rates, mask the potential for other unstudied vital rates to have stronger impacts on population growth or even opposing responses to climate variation (Figure 1c, inset). Several studies have shown that climate responses differ among developmental stages, with some stages more sensitive to projected climate changes than others (Levy et al., 2015; McLaughlin & Zavaleta, 2012; Radchuk, Turlure, & Schtickzelle, 2013; Woods & Wilson, 2013). For example, Radchuk et al. (2013) found that warming improved performance across all life stages of a butterfly, except for overwintering larvae which had lower survival under warming. Interestingly, population growth was most sensitive to this life cycle transition, and population growth rates decreased with warming despite positive effects on all other life stages. However, none of the studies we reviewed assessed climate effects across the entire life cycle of an organism. In addition to differences among life stages, different types of vital rates, such as survival, growth, or fecundity, could have opposing responses to climate change (Bestion, Teyssier, Richard, Clobert, & Cote, 2015; Doak & Morris, 2010; Peterson et al., 2018), a possibility that becomes more likely when populations across a species' entire range are considered (Villellas, Doak, García, & Morris, 2015). The climate responses of a single vital rate or life stage may therefore have little influence on population growth, and thus patterns of distribution or abundance, leading to biased forecasts of species range shifts.

A landscape demography approach (Gurevitch, 2016) could address these challenges by incorporating data on all of the vital rates needed to predict population growth rates (Figure 4). Landscape demography approaches have the advantage of incorporating density dependence, thereby allowing the prediction of changes in equilibrial abundance, which provides much more information on the ecological impact and conservation risk for populations throughout the species range (Ehrlén & Morris, 2015). Another advantage of these models is that their output can be directly linked to potential conservation actions, by identifying the vital rates, life stages, or environmental changes to which population growth or extinction risk is most sensitive (Merow et al., 2014). Although a few studies have used demographic models to forecast species' range responses to climate change (Fernández-chacón et al., 2011; García-Callejas, Molowny-Horas, & Retana, 2016; Merow et al., 2014), or used demographic models in conjunction with traditional SDMs (Swab, Regan, Matthies, Becker, & Bruun, 2015; Ulrey, Quintana-Ascencio, Kauffman, Smith, & Menges, 2016), none have yet included LA in vital rate responses to climate, most likely because of the additional data needed to separately estimate vital rate responses to climate drivers within multiple populations. Incorporating LA will thus require multisite demographic studies as well as methods to interpolate vital rate/climate relationships throughout the species' range. Although this approach is necessarily data-intensive, requiring experimental climate manipulations or substantial spatial and temporal replication, we advocate its adoption in well-studied or experimentally tractable systems for which these data can be collected.

Finally, individual-based models provide perhaps the most flexible, albeit computationally intensive, frameworks for incorporating local adaptation, dispersal, and demographic stochasticity into range and abundance predictions. For example, RangeShifter is a platform that combines demographic models with individual-based variation in dispersal (Bocedi et al., 2014), and could be used to incorporate local adaptation by separately modeling intraspecific groups with differing environmental tolerances. Similar but separate modeling frameworks include dynamic vegetation models (DVMs), which employ approaches that generalize the strategy used in the original forest gap models (Snell et al., 2014). These models include both demographic processes as well as physiological attributes and competitive interactions among individuals (e.g., Vanderwel, Lyutsarev, & Purves, 2013; Gutiérrez, Snell, & Bugmann, 2016). Although there have been repeated calls to use this framework to predict climate change effects, including range shifts, and also suggestions that these models incorporate local adaptation (Anderegg, 2015; Keane et al., 2001; Snell et al., 2014), we could find no existing studies using this framework that have done so yet.

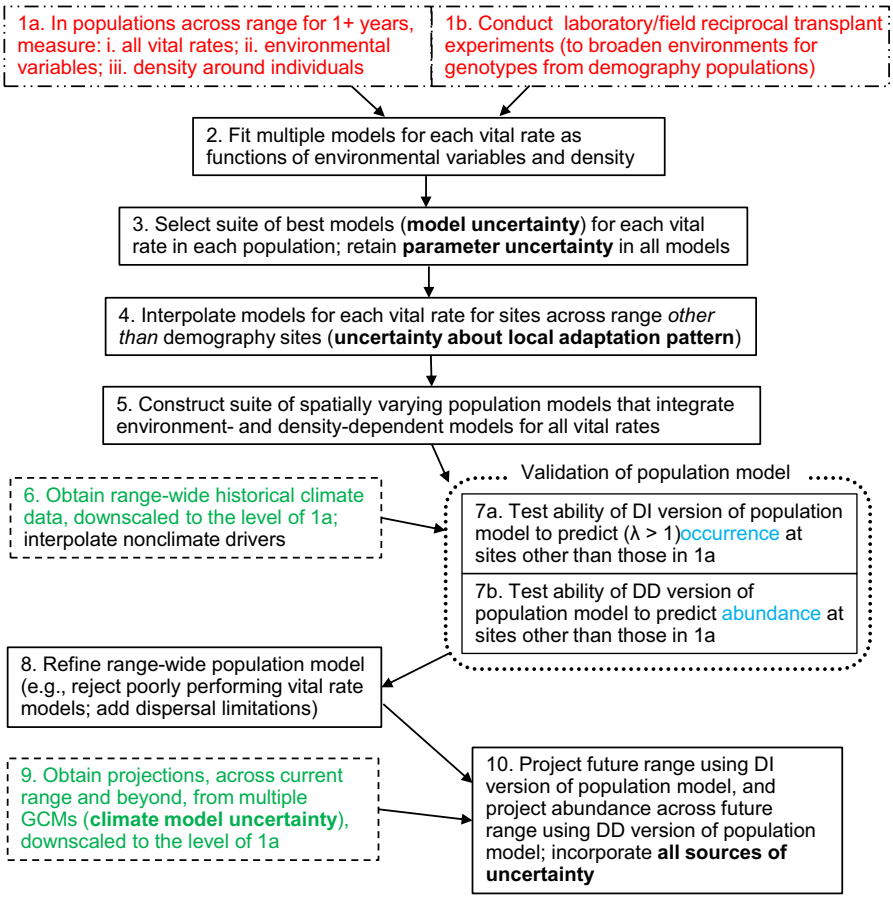


FIGURE 4 This flowchart outlines a protocol for using a landscape demography approach to project future distribution and range-wide abundance given local adaptation. Statistical and modeling steps are in solid boxes, demographic data are in dash-dotted boxes, occurrence/abundance data from nonstudy sites are in dotted boxes, and historic and projected climate data are in dashed boxes. DD: density-dependent; DI: density-independent; λ: low-density population growth rate. Sources of uncertainty are in bold

4 | BUILDING TOWARD A GENERAL FRAMEWORK

As we have reviewed, there are myriad approaches and challenges to incorporating LA into climate response forecasts and thus attempting to improve our predictions. In the face of this complexity, it is important to return to the importance of trying to do so in the first place. First, there is overwhelming evidence that LA to climate is strong and extremely common in natural populations (Bocedi et al., 2013; Fournier-Level et al., 2011; Jump & Peñuelas, 2005; King et al., 2017; Savolainen et al., 2007). Second, if LA to climate has the effects proposed by us and by many others (Atkins & Travis, 2010; Bocedi et al., 2013; Valladares et al., 2014), it will profoundly alter general patterns of climate change response away from those predicted by the dominant paradigm of "trailing-edge/leading-edge" responses (Hampe & Petit, 2005 has been cited 1,390 times and "trailing-edge leading-edge climate change" has 52,300 results on Google Scholar). While this paradigm is a powerful way to conceive of climate responses, if LA is strong, it may also severely underestimate the impacts of climate change on the range, density, and genetic diversity of species.

Addressing any of the challenges outlined above requires data that are unavailable for many organisms and unlikely to be collected within the timeframe needed to make accurate forecasts for conservation planning. For this reason, a high priority for climate change biologists must be to test general hypotheses about the effects of intraspecific variation in shaping species' responses to climate change. For example, does optimal climate or climate niche breadth vary predictably with latitude or elevation? Does incorporating LA tend to make species-level forecasts more or less pessimistic? Are warm or cold-adapted lineages at greater risk, and does this depend on dispersal rates? Searching for generalities will require consistent reporting of key data across studies (Table 2). For example, surprisingly few of the studies we reviewed here reported the geographic distribution, historical environmental conditions, and inferred climate responses for each intraspecific lineage considered. These data, collected across a range of taxa, are necessary for any meta-analysis seeking to understand the role of LA in shaping forecasted responses to climate change.

Studies that report the results of multiple models for the same system will further clarify the strengths and weaknesses of differing data sources and modeling approaches. For example, reporting the results of a species-wide distribution model alongside one incorporating intraspecific variation would allow tests of whether accounting for such variation alters either predictive accuracy or forecasted risk. Although this question has been the subject of a few individual studies (Angert et al., 2011; D'Amen et al., 2013; Pearman et al., 2010), developing a species-wide model is an important step in the model selection and validation process, and the inclusion of the results of such a model would

TABLE 2 General hypotheses that can be addressed by models incorporating intraspecific variation in climate responses ("G × E") into species' distribution forecasts. Data required and examples of studies that evaluate each hypothesis. For hypotheses addressed by at least ten models, we report the number of models out of the total number that find support for the hypothesis (Supporting Information Appendix S2). We also suggest steps for future studies to test these hypotheses. Consistent reporting of key data across many studies are necessary for stronger tests of these hypotheses in the future

Hypothesis	Evaluation method	Examples	Current understanding	Suggestions
Intraspecific groups differ in responses to climate change	Climate responses in performance for a set of intraspecific lineages	O'Neill et al. (2008)	14/15 models in support	Statistical tests for lineage × climate interactions
Including G × E increases model accuracy	Validation of models with and without G × E	Pearman et al. (2010)	17/24 models in support	Compare intraspecific models to a species-wide model, perform independent model validation
Including G × E increases forecasted risk of species-level declines	Species-level forecasts from models with and without G × E	Cacciapaglia and van Woesik (2018)	10/23 models in support	Compare intraspecific models to a species-wide model, aggregate lineage-level forecasts to understand species-level risk
Climatic optima (breadth) are correlated with historical climate means (variability)	Inferred performance/climate relationships and historical climate conditions for each lineage	Angert et al. (2011)	Insufficient evidence	Statistical tests for correlations between climate responses and climate of origin across lineages
Warm-adapted lineages are at greater risk than cold-adapted lineages	Lineage-level forecasts and historical climate conditions or inferred performance/climate relationships	Hu et al. (2017)	Insufficient evidence	Statistical tests for correlations between forecasted risk and climate of origin or climate optima across lineages, with and without dispersal
Range-edge lineages are at greater risk than centrally occurring lineages	Lineage-level forecasts and current distributions	Wang et al. (2006)	Insufficient evidence	Statistical tests for correlations between range position and forecasted risk, with and without dispersal

allow more general tests of the effects of LA on species forecasts. Similarly, studies that incorporate intraspecific variation through response functions or mechanistic models could easily compare these results to SDMs fit to more readily available occurrence data (e.g., Oney, Reineking, O'Neill, & Kreyling, 2013).

5 | CONCLUSIONS

Incorporating LA in climate responses has the potential to greatly improve forecasts of species' responses to climate change. A wide range of data sources to estimate intraspecific variation in climate responses and methods to incorporate this information into species-level forecasts already exist. However, current approaches can be substantially improved by rigorously testing and validating intraspecific variation in climate responses across a range of geographic scales and thoroughly evaluating the effects of uncertainty associated with LA on forecasts. Landscape demographic models and dynamic evolutionary models, while data-intensive, each hold great promise for addressing the effects of climate change across the life cycle and of future evolutionary processes. Finally, we hope that by continuing to improve and apply these methods across a wide range of taxa, we can begin to evaluate more general hypotheses for the ways in which LA may alter species' responses to climate change.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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