New Phytologist

Forum

Commentary

Moving forecasts forward

Forecasting how species will be impacted by climate change is one of the greatest challenges facing ecologists today. Thousands of forecasts have been published for species across the globe and, together, are the basis of global estimates of the overall impact of climate change on biodiversity (e.g. Thomas *et al.*, 2004). Yet until recently, there has been a disconnect between species' forecasts, which largely consider a single species-wide climate niche, and population studies, which have repeatedly shown strong intraspecific differences in climate tolerance (reviewed in Jump & Peñuelas, 2005; Bocedi *et al.*, 2013). For example, populations or ecotypes of a given species may be locally adapted to climate, such that they perform best under different climate conditions, resulting in a mosaic of responses to climate change across a species' range. This type of intraspecific variation in climate responses could dramatically alter species-level forecasts of performance or distribution in future climates (Fig. 1). However, relatively few studies have included intraspecific variation in forecasts, and most have been based on observational patterns of occurrence rather than robust experimental data, leading to calls for better approaches to include intraspecific variation in species forecasts (Valladares *et al.*, 2014; DeMarche *et al.*, 2019; Smith *et al.*, 2019). In this issue of *New Phytologist*, Patsiou *et al.* (2002; pp. 525–540) meet this challenge, presenting an innovative approach that combines experimental estimates of climate tolerances with careful model validation to explore how ecotypes of Aleppo pine (*Pinus halepensis*) will respond to forecasted climate change locally and throughout the species range.

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One of the main challenges to including intraspecific variation in species' forecasts is simply obtaining data on how climate tolerances may vary throughout a species' range. Most forecasts are based on correlations between species' occurrence records and historical climate data, which are used to estimate a species' climate niche (i.e. species' distribution models (SDMs); Franklin, 2009). Although occurrence data are readily available for many species, they do not allow strong tests for intraspecific differences in climate tolerances. An alternative approach, taken by Patsiou *et al.*, is to leverage experimental data on the performance of multiple populations when grown in a common set of environments (e.g. reciprocal transplant or common garden experiments). In their study, Patsiou *et al.* combine data on the height of Aleppo pine from nine common garden experiments, representing 82 populations in five ecotypes, to test ecotype-by-climate interactions and uncover ecotype-specific responses to forecasted climate change. Specifically, they test the hypothesis that ecotypes will respond differently to climate conditions across common garden sites, and that these differences will be consistent with local adaptation, in which each ecotype performs best under local climate conditions. To do this, Patsiou *et al.* use an analysis framework that allows them to compare how well different climate variables can explain the variation in ecotype performance across gardens, to identify the most important climate drivers for this species. They then estimate how these climate variables influence height for each ecotype separately as well as for the species as a whole, and use these to forecast how climate change will alter local and range-wide patterns of performance.

This approach reveals several nonintuitive patterns. First, although ecotypes of Aleppo pine differ strongly in their responses to climate, this is largely driven by precipitation rather than temperature. Responses to precipitation are strongest in mesic wet-summer ecotypes with their height decreasing substantially in dry environments. Conversely, ecotypes from warmer, drier environments tend to show weak responses to precipitation. Temperature, however, has similar positive effects on height across the species range. Second, differences among ecotypes are not always consistent with local adaptation. For example, only mesic ecotypes are predicted to have an advantage in their local climates. Taken together, Patsiou *et al.* uncover a complex picture of climate tolerances range-wide, and this is reflected in forecasts of future performance. Under projected warming and drying, Patsiou *et al.* show that locally-adapted mesic ecotypes are increasingly outperformed by dry-adapted ecotypes. Further, they predict the largest declines in height to occur in the mesic portions of the range. This pattern is in stark contrast to the general expectation that climate change will have the biggest impact in the warmest and driest portion of a species' range (i.e. the 'trailing edge'). Only by understanding the different sensitivities to climate in mesic vs dry-adapted ecotypes are Patsiou *et al.* able to discover this unexpected pattern, highlighting the importance of explicitly incorporating intraspecific variation in climate responses into species forecasts.

In addition to these insights, perhaps one of the greatest strengths of the work by Patsiou *et al.* is their careful approach to model validation and uncertainty in their predictions. The utility of any forecast is dependent on its precision, and sources of forecast uncertainty – from future climate projections to rates of dispersal – must be acknowledged and quantified wherever

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This article is a Commentary on Patsiou *et al.* (2020), **228**: 525–540.

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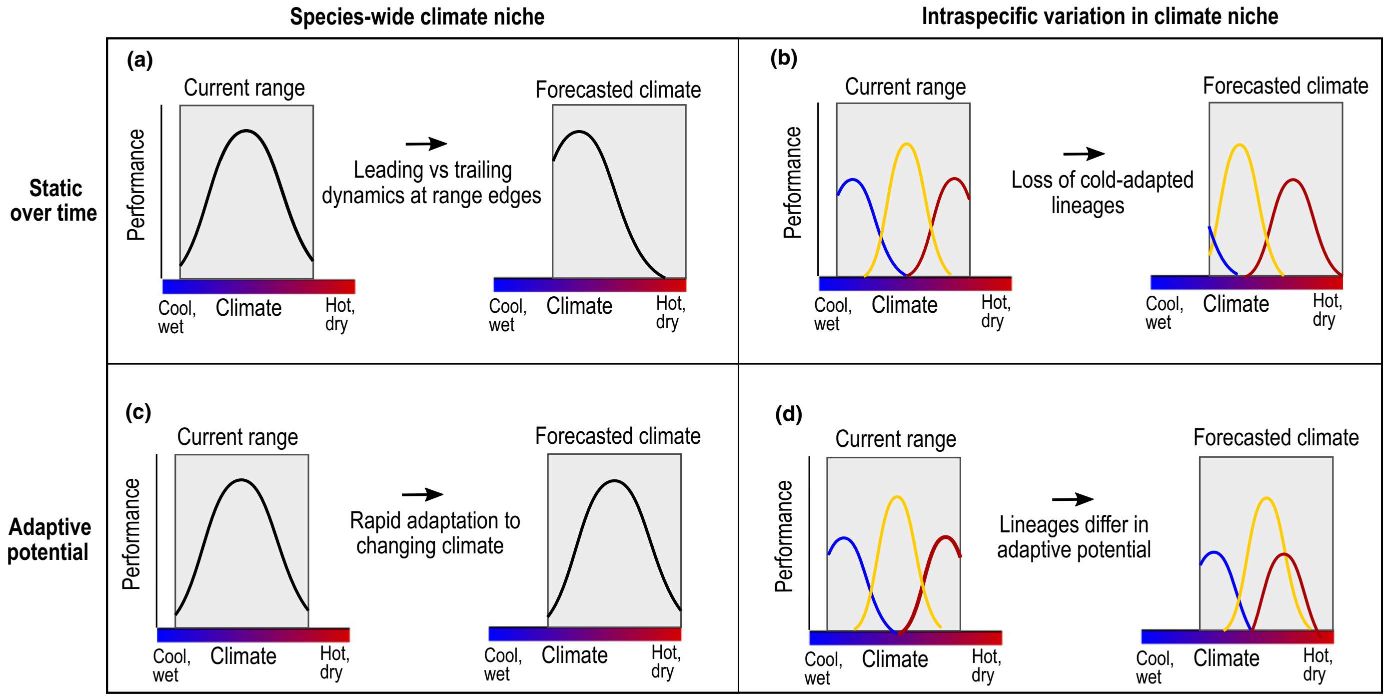

Fig. 1 Conceptual diagram showing how intraspecific variation (b, d) and adaptive potential (c, d) can be included individually or combined to improve forecasts of species' responses to climate change. Panels illustrate how climate responses estimated in the current species' range can shape patterns of performance in a hypothetical warmer and drier future climate. (a) Most forecasts assume a single species-wide climate response, suggesting that performance will increase at cooler 'leading' range edges and decrease at warmer 'trailing' range edges. (b) Instead, studies such as Patsiou *et al*. (2020; pp. 525–540) published in this issue of *New Phytologist* suggest that intraspecific lineages differ in their climate responses, which can result in the loss or spread of different lineages (e.g. loss of cold-adapted blue lineage, spread of warm-adapted red lineage) depending on rates of dispersal. (c) Some forecasts incorporate adaptive potential, allowing climate responses to evolve over time and track shifting climate conditions. (d) A promising future direction is to combine these approaches to account for differences in adaptive potential among lineages, such as upper limits to heat or drought tolerance (e.g. no evolutionary response in warm-adapted red lineage) or reduced genetic variation at range edges.

possible (Buisson *et al.*, 2010). Incorporating intraspecific variation into forecasts requires making additional choices, such as how to group individuals with shared climate responses, that can also contribute to forecast uncertainty (Martin *et al.*, 2019). However, the uncertainty due to intraspecific variation has received much less attention relative to other aspects of forecast models (DeMarche *et al.*, 2019). In their study, Patsiou *et al.* use a series of complementary approaches to thoroughly probe the predictive accuracy and precision of their models. In addition to commonly-employed cross-validation methods, which capture the ability of models trained on a randomly selected subset of the data to predict the remaining data points, Patsiou *et al.* also take the important step of testing their ability to predict performance in five new common garden experiments including 75 new populations. This validation step, based on independent datasets, confirms the ability of their ecotype-specific climate models to successfully extrapolate to new populations and environments, a necessary step when generating range-wide forecasts under future climate conditions. In addition, Patsiou *et al.* also use a bootstrap approach to map the standard deviation in their model predictions, making explicit the uncertainty in forecasted performance due to statistical uncertainty in model parameters. This kind of comprehensive validation process remains all too rare, but can yield important insights. For example, Patsiou *et al.* are able to identify specific ecotypes and climate conditions with greater forecast uncertainty, providing potential targets for future research.

Together, the work by Patsiou *et al.* is a notable advancement in how we estimate and validate species' responses to climate change. Importantly, this type of approach can be used to address a wide range of basic and applied questions, such as: how do geographic and environmental factors structure intraspecific variation in climate tolerances? Are populations more or less vulnerable in different portions of the range or types of climate conditions? Are particular ecotypes expected to dominate in future climates? and what is the potential for assisted migration to buffer species-wide impacts of climate change? Looking forward, this type of approach could also be modified to incorporate on-going evolutionary adaptation in addition to current patterns of intraspecific variation (Fig. 1d). To date, forecasts based on intraspecific responses from common garden experiments have largely been limited to economically important trees, like Aleppo pine, with longer generation times and less potential for rapid evolution in future climates (e.g. Wang *et al.*, 2010). However, incorporating future evolution will be important for forecasting climate change responses for species with shorter generation times and for all species over longer timescales. Several studies have used common garden approaches to quantify intraspecific variation in climate tolerances for species with shorter generation times (Wilczek *et al.*, 2014; Anderson *et al.*, 2015), and forecast models are being

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developed that include the potential for future evolutionary change (Bush *et al*., 2016; Cotto *et al*., 2017), suggesting that this may be a promising avenue for forecasting climate change impacts in the future.

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