

Disequilibrium and relaxation times for species responses to climate change

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ABSTRACT

Climate change is widely expected to pose a threat to many of Earth's plant and animal species. Based on climate models, a multitude of studies project that certain species will not be able to migrate fast enough to keep up with changing environmental conditions, presenting a greater risk of their possible extinction. However, many of these studies are based on correlative climate niche models that represent the current living conditions of species and may not consider their ability to tolerate projected changes in future climate, including the stimulative effects of rising CO₂ for plant growth and drought tolerance. SDMs also are not usually run with sufficiently detailed spatial data to account for refugia. These and other aspects of model-based niche studies can potentially combine to mischaracterize the risk to species due to climate change. Even a SDM that perfectly predicts future equilibrium geographic range following climate change, however, does not yield a direct estimate of extinction risk. The key question is "What is the transient response to a climate disequilibrium situation?" The concept of relaxation is introduced to evaluate time-scales for responses at the trailing edge of species' ranges. Simulation of relaxation at a forest ecotone shows the relaxation response in some cases can be hundreds of years. A classification of relaxation responses based on tolerance and dispersal ability is proposed as a second stage analysis for SDM studies.

1. Introduction

A number of studies postulate that anthropogenic climate change will lead to mass extinctions (Bakkenes et al., 2002; Parmesan, 2006; Parmesan and Yohe, 2003; Thomas et al., 2004; Thomas and Williamson, 2012; Urban, 2015). The most common approach used for these studies is for researchers to first examine the current geographic range and climate of a given species after which they project how future changes in climate may impact the geographic ranges. Models of factors governing species geographic ranges, called species distribution models (SDMs), climate envelope models, or niche models, are developed statistically and are used to characterize current and projected geographic ranges (Busby, 1988). Comparison between a species' current and projected climate zones (see Loarie et al., 2009) is then the basis for estimating extinction risk (Fig. 1). If climate change leads to a non-overlapping shift in a species' range (Fig. 1a) and the species cannot migrate fast enough to keep pace with the shift, it is assumed that the species will be "committed to extinction" (per Thomas et al., 2004). Another possible outcome is a range reduction. In this case (Fig. 1b), a smaller geographic range is presumed to cause a population decline, thus increasing extinction risk for that species, though not necessarily dooming it. This framework is widely used (e.g., Bakkenes et al., 2002; Breshears et al., 2008; Davis and Shaw, 2001; McKenney et al., 2007), with studies in the thousands (Booth, 2017).

A distribution model is a statistical response surface for predicting where a species will be found, either currently or in the future. The variables for predicting the distribution of a species, such as minimum winter temperature, elevation, and precipitation, are selected and a model is developed (Elith et al., 2010). However, some aspects of this approach have been questioned (e.g., Botkin et al., 2007; Dormann, 2007; Yackulic et al., 2015), it may have uncertainty resulting from method choice (Buisson et al., 2010), uncertainty in forecasts can be large (e.g., Wenger et al., 2013; Wiens et al., 2009), and results have rarely been validated (Botkin et al., 2007). Even if bioclimate models capture the realized niche, they may not make reliable predictions about the fundamental niche (Anderson, 2013; Booth, 2017; Loehle and LeBlanc, 1996) which is the climate, soils, vegetation, and other features that an organism needs for basic survival. The realized niche, in contrast, is the environment where the organism is able to persist despite biotic interactions and thus where it is actually found. The realized niche is typically much smaller, or more restrictive, than the fundamental niche and is what SDMs capture. While a few studies have evaluated both (e.g., Booth et al., 1988; Briscoe et al., 2016; Tingley et al., 2014), most have not (Booth, 2017). Thus, bioclimatic models may underestimate environmental tolerance (Araújo and Pearson, 2005; Booth, 2017; Catullo et al., 2015; Loehle, 2014; Loehle and LeBlanc, 1996; Sax et al., 2013).

A central difficulty with this approach was pointed out by Araújo

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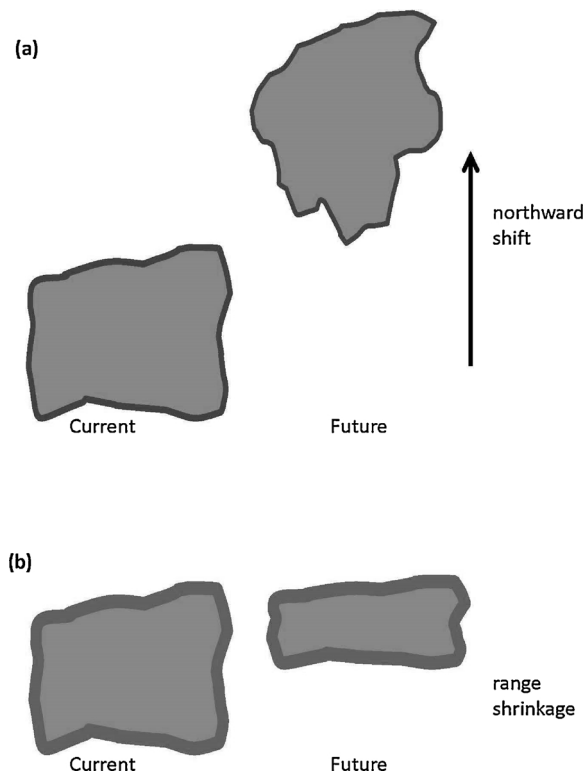


Fig. 1. Evaluation of current vs. projected future climate zones. (a) Poleward or upward shifts lead to non-overlapping current and future climate zones, causing extinction of species; (b) Reduction in range leads to increased risk for a species.

and Peterson (2012): extinction risk is not an explicit target of the SDM modeling approach. That is, an SDM analysis applied to future climates only predicts future equilibrium conditions and says nothing about what will happen between now and the achievement of equilibrium. If, at the trailing edge, a species can tolerate the new climate while it migrates to the new zone, then the distribution shift does not represent an increased risk of extinction. While it is known that the models are explicitly equilibrium analyses (Araújo and Peterson, 2012; Pearson and Dawson, 2003), the cautions about dynamics and tolerance of new conditions are often ignored (Pearson and Dawson, 2003) even in the most recent studies (Booth, 2017).

The problem here is not that SDMs are unrealistic (though they may be). Even a perfect future forecast does not inform us about transient responses. Another way to put this is that it is implicitly assumed that any no-overlap zone by some date (say 2100) implies reduced abundance or local extinction in that zone. This implicit response is illustrated in Fig. 3a. Growth is assumed to decline until the species cannot persist below the coldest or above the warmest temperatures (N and S respectively in the figure) implied by the current range. Thus, as soon as the temperature shifts geographically, species are assumed to find themselves in a lethal zone and quickly perish. However, this approach represents a conflation of the fundamental and realized niches. The growth response implied by Fig. 3a is not observed in nature except perhaps at the coldest and driest extremes for life where competition is minimal. Everywhere else, a species will encounter competitors long before it has a growth rate near zero (N or S in Fig. 3a). Interestingly, trailing edge retreat due to warming has so far been difficult to document, especially for plants (Intergovernmental Panel on Climate Change (IPCC), 2014; Lenoir and Svenning, 2015; Loehle, 2018). This suggests that inertia might exist due to species' tolerances of altered climate and other factors.

1.1. Mechanisms for disequilibrium

The dynamics of response to a change in climate should be considered when estimating extinction risk (Jackson and Sax, 2010). The time required to return from disequilibrium to a new equilibrium (“relaxation time”) can be prolonged (Cole, 1985, 2009; Jackson and Sax, 2010; Loehle, 2000a; Loehle and LeBlanc, 1996) due to environmental tolerance. In addition, habitat complexity can create microclimatic refugia (Austin and van Niel, 2010; Dobrowski, 2011; Scherrer and Körner, 2010) which typically are not accounted for in niche models. For example, alpine plants found refugia during past warmer interglacials (Gentili et al., 2015), which allowed a rare endemic plant in the Alps to persist over the past 21,000 years (Patsiou et al., 2014). Lenoir et al. (2013) documented the extent to which topography creates strong spatial buffering (refugia) for plants in northern Europe. Keppel et al. (2012) summarized over 2000 studies on refugia.

Growth models have been used to predict effects of climate change on ecosystems and provide a test of the range shrinkage prediction. While these models do not have the status of experiments, they are based on mechanisms of plant growth. Growth models can incorporate effects of future increases in CO₂ which are likely to increase growth rates, decrease water stress, and increase the optimum temperature for photosynthesis (Tian et al., 2010; Wertin et al., 2010). These models generally predict enhanced growth over the coming century, especially if elevated CO₂ growth enhancements are included in the model (Loehle, 2011, 2014; Keenan et al., 2011; Cheaib et al., 2012; Kearney et al., 2010; Morin and Thuiller, 2009). Thus, rising CO₂ could also increase inertia for plants.

1.2. Historical evidence for climate tolerance

Tolerance of fluctuating climate as well as SDM reliability can be tested using historical data. The bioclimatic niche equilibrium assumption leads to predictions that 1) rapid past climate shifts should have caused extinctions, and 2) very warm past conditions should have had reduced biodiversity and caused extinctions due to the exceedance of species' thermal tolerances, especially in the tropics. Neither of these two predictions, however, appears to have much support in the paleoliterature.

A hind-cast of the location of five mammalian species' glacial refugia in North America based on current bioclimatic niche relations (Davis et al., 2014) found that the models predicted refugia far south of the actual fossil locations for all five species. This is either due to the climate envelope models or the simulated climates. Similarly, Tyrberg (2010) showed that, during the last interglacial period, multiple sites that were 2 °C warmer than present had the same avifaunal assemblages as today rather than something radically different, as implied by some models.

Toward the end of the last glacial period, rapid warming occurred multiple times, including rates much larger than has been observed over the past 100 years (Hof et al., 2011). Yet few extinctions have been identified in these periods (Hof et al., 2011), especially for plants such as trees in particular (Loehle, 2006, 2007). While some end-Pleistocene extinctions are known, they appear to have been largely precipitated by human hunting pressure (Hof et al., 2011) because their timing coincided with human arrival in each location and fossils show evidence of hunting (see citations in Loehle and Eschenbach, 2011). This evidence lends support to the hypothesis that species can be in climatic disequilibrium without extinction.

Another line of evidence for potential climate tolerance consists of the historical biogeography of endemics. In eastern North America, there are almost no endemic plants in glaciated regions due to a lack of sufficient time for endemics to have evolved since ice retreat, yet endemics can be found within a few miles of the historic ice sheet margin (Davis and Shaw, 2001; Loehle, 2006, 2007). Consequently, the hundreds of narrow endemic plants in this ice margin region likely survived

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