Commentary

Adding edaphic nuance to species distribution models complicates predictions of range shifts

Species have several possible responses to directional climate change: cope with environmental change *in situ* either via phenotypic plasticity or adaptive evolution, or migrate to track suitable environmental conditions as previously less habitable environments become more suitable (i.e. range shifts; Zettlemoyer & DeMarche, 2021). Ecologists generally expect species to shift poleward and upward with climate change, but nonclimatic factors can complicate this story (Ford & HilleRisLambers, 2020). Accordingly, most species distribution models (SDMs) to date have used climatic variables to assess future suitable habitats (Guisan *et al.*, 2017) despite the existence of other factors that might vary with latitude, such as edaphic conditions. In a recently published article in *New Phytologist*, Ni and Vellend (2023, doi:10.1111/nph.19164) compare predictions of range shifts between SDMs that incorporate climate conditions, soil properties, and a combination of the two. Building a suite of ensemble models predicting current and future distributions for 1870 species native to Eastern North America, the authors demonstrate that SDMs incorporating both climate and soil properties predict reduced range expansions relative to SDMs parameterized with climate only.

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Within a plant species' range, geographic environmental variation can structure local adaptation and that taxon's geographic range limits (Benning & Moeller, 2021). However, knowing what factors cause a range limit to occur is difficult, especially when those factors are correlated. Soils, like temperature and precipitation, can vary substantially at continental scales, ranging from the water-logged, post-glacial soils of high latitudes to more fertile southerly soils. Even if climate warming shifts suitable climate conditions such as air temperature or precipitation poleward (or upward in alpine environments), edaphic conditions beyond the current range limit will also need to be suitable to facilitate migration.

Despite the historical assumption that climatic gradients will override the effects of edaphic variables in SDMs (Heikkinen *et al.*, 2006), several studies have incorporated climate and edaphic predictors into SDMs at small spatial scales with relatively homogenous soils (Bertrand *et al.*, 2012; Le Roux *et al.*, 2013; Beauregard & de Blois, 2014; Buri *et al.*, 2017; Chauvier *et al.*, 2021). They all find that soil properties play a critical role in determining plant distributions. For instance, *Quercus pubescens* is excluded from a climatically suitable area when soil pH is included as a predictor (Bertrand *et al.*, 2012). This suggests that soil constraints modify projections of future suitable habitat. Other research has focused on the suitability of soil from beyond individual species' contemporary ranges for fitness, independently of climate (Brown & Vellend, 2014; Carteron *et al.*, 2020). Ni and Vellend expand these approaches to address whether soil suitability beyond species' range might constrain migration at a continental scale. Although climate (mean annual temperature) remained the most important predictor of species' distributions, several soil characteristics (saturated water content and soil order – the latter reflecting acidity and nutrient content) had comparable effects on projected range sizes.

The effects of these soil characteristics varied with species characteristics. Wetland species demonstrated greater sensitivity to edaphic parameters as the authors expected based on wetlands' unique soil environments. Similarly, climbers and trees were less sensitive to edaphic parameters than forbs and shrubs; this is potentially due to lower reliance on soil properties from aerial growth and deep roots, respectively.

Importantly, the study finds some of the first evidence that soil variables could reduce the magnitude of climate-driven range shifts for many Eastern North American species. This result adds needed nuance not only to models of potentially suitable habitats but also highlights potential complications for species' range shifts under climate change. For instance, many studies detect migration lags under climate change, wherein species do not keep pace with the rate of climate change due to a lack of dispersal, establishment at range edges, or extinction lags of the resident species (Alexander *et al.*, 2018). Ni and Vellend suggest that unsuitable soil environments could serve as a barrier to establishment and persistence beyond contemporary range edges unless altered climate and vegetation dynamics make the soils more suitable for migrating species over time. Indeed, Ni and Vellend suggest that climate-only models might overestimate increasing species richness in poleward habitats because their soils are likely to be unsuitable for migrating species. As experiments investigating beyond-the-range limit population dynamics become more popular (Hargreaves & Eckert, 2019), incorporating edaphic parameters could better inform the potential for migration and persistence beyond range edges (Fig. 1). Moreover, edaphic SDMs could help

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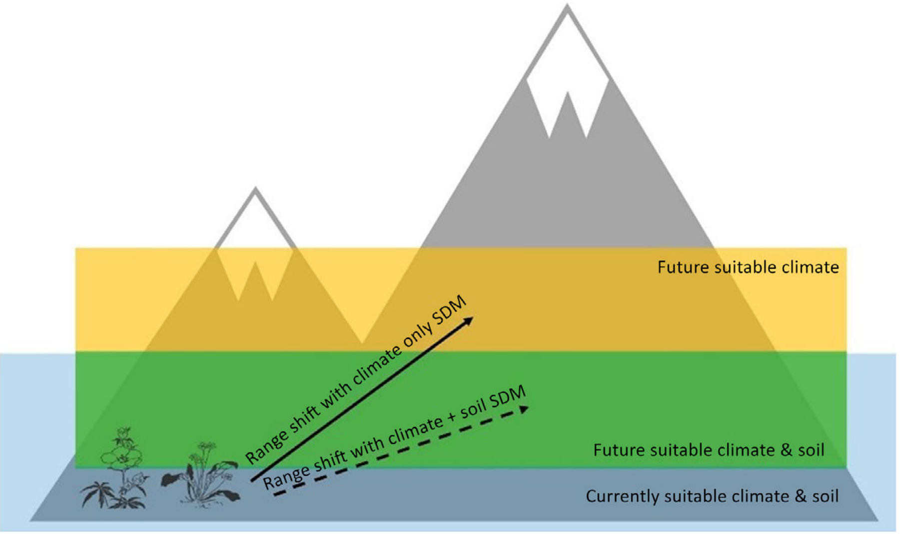

Fig. 1 Magnitude of range shifts (here shown as a low-elevation species migrating upward in elevation) might be limited by both climate and edaphic parameters. Species that survive under current climate and edaphic conditions (blue) are projected to shift their ranges upward (or poleward; solid arrow) into more suitable climates (yellow), but this shift might be constrained (dashed arrow) to areas that also host suitable soil conditions (green). (Species distribution model (SDM))

locate sites with soils analogous to a species' current habitat, aiding in the identification of suitable refugia for vulnerable species.

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