Soil Effects on Vegetation Dynamics Under Climate Change 1 2 Ming Ni^{1,2}, Mark Vellend³ 3 4 ¹Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), Department of Biology, 5 Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark 6 ²Department of Botany, University of Wisconsin, Madison, WI, USA 7 ³Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, J1K 2R1 Canada 8 9 Corresponding author: Ming Ni (niming.anhui@gmail.com) 10 11 Orcid: Ming Ni https://orcid.org/0000-0002-5180-1049; Mark Vellend https://orcid.org/0000-12 0002-2491-956X 13 14 **Keywords:** Soil, climate change, vegetation, community composition, range shifts, niche 15 **Acknowledgement:** This study was supported by the Natural Sciences and Engineering Research Council of Canada, and Danish National Research Foundation (Center for Ecological 16 17 Dynamics in a Novel Biosphere, grant DNRF173).

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Abstract: While predictive models of contemporary vegetation change often emphasize climate as the main driver, soil properties are increasingly recognized as critical mediators. This review synthesizes evidence on climate-soil interactions from diverse fields (e.g., paleobiology, species distribution modelling, and plant-soil feedbacks) across multiple scales. We propose a framework capturing how soil-climate correlations and species' niches shape vegetation change, revealing several important mechanisms of climate-soil interactions. At local scales, communities restricted to unusual soils often resist thermophilization, and high soil heterogeneity can further buffer climate impacts. However, emerging soil-climate combinations may generate novel ecosystems. At biogeographical scales, soils constrain species' range limits and migration rates, yet most evidence comes from temperate regions. For tropical-to-temperate transitions, we predict that soils might instead accelerate migration, based on greater soil fertility in the temperate zone. The distributions and climate sensitivities of soil microbes may not align with those of plants, posing challenges for predicting plant range shifts. Mechanistic species distribution models linking traits and demographic processes to soil properties offer a promising path to improve predictions. Our synthesis shows that understanding soil-vegetation-climate interactions is essential for accurate predictions of future plant distributions, community composition, and extinction risk in a changing climate.

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1. Climate change and vegetation dynamics

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Global average surface temperatures have risen by 1.0-1.2 °C since pre-industrial times (1880-1900), with models predicting additional increases of 1.4-4.4 °C during the 21st century (Lee et al., 2023). This rapid climate change is anticipated to have profound impacts on global vegetation: At the local scale, increasing temperatures and changing precipitation regimes will alter plant community composition, with changes in abundance depending on species' adaptations to different climatic conditions (Danneyrolles et al., 2019; Fastovich et al., 2025). On broader scales, many plant species are likely to migrate to higher latitudes or altitudes to track rising temperatures (Chen et al., 2011; Lu et al., 2025). Current predictions at both local and broad scales are primarily based on plant species' climatic niches (Pacheco-Riaño et al., 2023; Thuiller et al., 2011; Zhu et al., 2024), typically ignoring non-climatic factors, particularly soil properties, which can significantly impact plant fitness (Hulshof & Spasojevic, 2020). Soil provides plants with water, nutrients, and physical support, and plant performance varies substantially along soil gradients in a species-specific way (Hulshof & Spasojevic, 2020; Joswig et al., 2021; Kruckeberg, 2004; Laliberté et al., 2013). Given the high spatial heterogeneity and multitude of soil properties (Box 1), which show frequent correlations with latitude or altitude, soil properties might play a crucial role in shaping plant responses to climate change (Bertrand et al., 2012; Ford & HilleRisLambers, 2020; Lafleur et al., 2010; Ni & Vellend, 2024a; Sanczuk, Verheyen, et al., 2024; Zhu et al., 2024). Despite increasing recognition of the importance of soil (Cartwright, 2019; Corlett & Tomlinson, 2020; Hagedorn et al., 2019), we lack a synthetic understanding of how soil heterogeneity shapes plant responses to climate change across spatial scales. This review integrates recent theoretical and empirical advances to illustrate how soil properties mediate

vegetation responses to warming, focusing on two linked spatial scales most often treated independently in the literature: local-scale community composition shifts and large-scale plant migration. We propose a framework in which available environmental soil-climate space and the shapes and positions of plant environmental niches in this space are central to predicting plant community composition and distributions under climate change, while recognizing that plant-soil-climate feedbacks may further modify outcomes. The resulting insights have major implications for forecasting future vegetation dynamics and for biodiversity conservation.

2. Soil effects on local shifts in plant community composition

Climate change is expected to reshape local plant communities, leading to an increase in the abundance of species adapted to warmer temperatures (potentially including new arrivals), while populations of cold-adapted species may decline. Such "thermophilization" has been observed in multiple studies (Danneyrolles et al., 2019; Feeley et al., 2020; Zhu et al., 2024). However, shifts in the "temperature composition" of plant communities generally lag behind the pace of climate change (Pacheco-Riaño et al., 2023; Savage & Vellend, 2015). Here we adapt the graphical-conceptual approach of Jackson and Overpeck (2000) to illustrate several ways in which spatially heterogeneous soil properties may influence thermophilization, including some novel predictions.

In the following conceptual scenarios, we imagine one geographic area that has internal variation in soil and climatic conditions, but where soil characteristics remain constant over time while temperature increases. While some soil properties might be altered by climate change, our scenarios capture the likelihood of such changes being comparatively slow (Lambers et al., 2008; Weil & Brady, 2013). In this case, expected changes in community composition to depend on the

range of available climate and soil conditions in the present and the future, and how species niches (e.g., tolerance limits) map onto that environmental space (Figure 1) (Jackson & Overpeck, 2000).

In our first scenario, climate and soil are uncorrelated spatially, and species niches – defined independently of the range of environmental conditions available at a given moment in time – are distributed and oriented haphazardly in environmental space (Figure 1A). With respect to making predictions about future community change, one conclusion is immediately evident: We need knowledge of how species niches relate to environmental conditions beyond where we can currently make local field observations (Chevalier et al., 2024). Observations can only be made within the blue ellipses – the set of conditions currently in existence – but predictions depend on what will happen in the "no-analog" portion of the red ellipses that extends beyond the blue (conditions not currently in existence), a point frequently noted by paleoecologists (Jackson & Overpeck, 2000). In other words, species might thrive (or decline) in conditions that do not exist in a given area at present (and so are difficult to study), but that might exist in the future. We also need to know if species for which suitable conditions will be created are likely to arrive in our focal locality.

In nature, soil and climate conditions are likely to be correlated. For example, in temperate regions, both soil pH and temperature often decrease together with latitude and elevation (Weil & Brady, 2013). What are the consequences of such spatial correlations between climate and soil? In Figure 1B, species' niches are the same as in Figure 1A, as are the ranges of soil and climate conditions, but we have introduced a soil-climate correlation. Here the total volume of environmental space – both present and future – has been reduced, and more importantly, the degree of overlap between present and future has been reduced. This leads to the novel and as-

yet untested prediction of greater warming-driven species turnover when climate and soil gradients are correlated.

No-analog soil—climate combinations are conceptually aligned with the idea of novel ecosystems—species assemblages with no historical precedent that emerge under new abiotic and biotic conditions (Hobbs et al., 2006; Kerr et al., 2025). Numerous studies have analyzed how climate warming may generate novel climate regimes with potentially important effects on vegetation change (e.g., Chevalier et al., 2024; Li et al., 2018; Ordonez et al., 2016, 2024; Williams & Jackson, 2007), but explicit assessments of new soil—climate combinations remain scarce (but see Mäkinen et al., 2017). For example, if future warming drives temperate regions of eastern North America toward subtropical or even tropical temperature regimes, while soils remain unchanged (temperate soils are deeper, more fertile, and less acidic than typical tropical soils, Weil & Brady, 2013), we might expect novel ecosystems to emerge, supporting vegetation assemblages very different from those of today. A similar dynamic might be expected in Arctic areas that experience much warmer temperatures but retain thin, rocky soils (Figure 2).

Such non-analog soil—climate environments increase the uncertainty of predicting future ecological communities, as they require extrapolating beyond the range of current field observations (Chevalier et al., 2024; Williams & Jackson, 2007). Addressing this challenge will require a multi-pronged approach. First, more comprehensive assessment and mapping of potential novel soil—climate spaces is needed, which can be achieved using multivariate dissimilarity and novelty metrics (Mahony et al., 2017; Mesgaran et al., 2014). Second, process-based vegetation models, such as dynamic global vegetation models (DGVMs), that incorporate plant functional traits and adaptive strategies (with relevance to tolerance of different soil conditions) offer a more mechanistic basis for projecting responses under novel conditions

(Scheiter et al., 2013) than correlative methods. Traditional correlative approaches - such as community ordinations - statistically relate community composition to environmental conditions without incorporating the underlying physiological and demographic processes. In contrast, process-based models explicitly consider plant life cycles, competition, and dispersal, thereby capturing potential causal links among vegetation, soils, and climate, providing a basis for making predictions under unprecedented environmental combinations. For example, identifying plant traits that promote persistence in warmer Arctic environments with thin, rocky, organic soils could improve predictions of how tundra communities might reorganize in the future (Bjorkman et al., 2017, 2018). Finally, manipulative experiments that span a range of climate and soil contexts – such as warming experiments across soil gradients or reciprocal soil transplants – are critical to testing and validating model predictions, providing empirical evidence on how vegetation may respond under unprecedented environmental combinations.

Under a given set of available environmental conditions, the shapes of species' niches have a profound impact on the predicted consequences of warming. Focusing on just current conditions (blue ellipses) in Figure 1, the scenario where niches are more limited by climate (Figure 1C) and the scenario where they are more limited by soil (Figure 1D) have more or less the same initial relationship between community composition and environment: From bottom-left (let's say, cold and acidic soils) to top-right (warm and neutral soils), species dominance shifts from blue to orange, then to green, purple and red. Given various sources of ecological stochasticity and sampling uncertainty, we might have difficulty detecting any major differences in the vegetation-environment relationship in these two scenarios. But with warming, the different shapes of species' niches make a huge difference.

If species are limited more by climate than soil (Figure 1C), warming will lead to major vegetation changes, as has been observed in many studies (Feeley et al., 2020; Zhu et al., 2024). In contrast, if soil is more limiting than climate (Figure 1D), vegetation changes will be minimal. Indeed, some studies show that plant communities adapted to specialized soil environments are less affected by climate change (Cartwright, 2019; Corlett & Tomlinson, 2020). A long-term experiment in England found that native grasslands on infertile soils exhibited minimal change in response to prolonged climate treatments (warming, drought, watering), which had caused dramatic compositional shifts in other plant communities (Grime et al., 2000, 2008). Other studies found that the sensitivity of plant community composition to changes in the climatic water balance was lower on infertile serpentine soils than on more fertile soils (Harrison et al., 2015; Zhu et al., 2024). Studies using historical photographs over a period of decades (Kruckeberg, 2004) or using palaeoecological pollen analysis over millennia (Briles et al., 2011) have shown less pronounced vegetation changes on serpentine substrates than on other substrates. Assessing the generality of this conclusion will require empirical tests based on longterm vegetation monitoring in other edaphic contexts. Finally, if some species are more limited by soil and others more limited by climate, there is the potential for major ecological surprises (Williams & Jackson, 2007), such as reversals in species' positions along the correlated climatesoil gradient (Figure 1E), although we are unaware of empirical demonstrations of this possibility.

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So far, we have assumed independent variation in soil and climate, but further complexities arise if soil influences microclimate (Fridley et al., 2011; Certini & Scalenghe, 2023). The local temperature experienced by plants can depend on soil conditions. For example, high soil moisture can buffer soil temperature extremes, and deeper soils with greater water holding

capacity (e.g., more clay or organic matter content) can reduce the influence of drought (Fridley et al., 2011; Greiser et al., 2024). The latter can have a major impact in water-limited ecosystems facing increasing frequencies of drought (Abel et al., 2024; Clark et al., 2016; Ohlert et al., 2025; Wankmüller et al., 2024). More generally, high edaphic heterogeneity can provide multiple microclimatic environments, thus buffering climate change effects on plant communities, resulting in higher community stability at larger scales (García-Palacios et al., 2012; Greiser et al., 2024; Stover & Henry, 2019). Soil biotic properties can also interact with microclimate. The diversity of mycorrhizal associations can enhance vegetation stability by buffering against climate-driven resource fluctuations and promoting population stability and plant coexistence (Fowler et al., 2024; Janoušková & Jansa, 2025; Jia et al., 2021; Weber et al., 2025).

While soil properties can influence microclimate, the reverse is also true: climate change can, in the long run, influence soil properties. For instance, the replacement of coniferous by deciduous trees can increase soil pH due to differences in litter quality and decomposition (Lafleur et al., 2010), while warming tundra ecosystems can accelerate decomposition, thereby increasing nutrient availability (Koyama et al., 2013). Recent studies also highlight how climate change can substantially alter the soil microbiome (Delgado-Baquerizo et al., 2020; Guerra et al., 2021; Classen et al., 2015; Liu & He, 2022; Pugnaire et al., 2019; Sun et al., 2025), with potentially major impacts on plant-soil feedbacks and plant community assembly (Allsup et al., 2023; Bennett & Klironomos, 2019; Hagedorn et al., 2019; Ke & Wan, 2020; Pugnaire et al., 2019; Putten et al., 2013; Tedersoo et al., 2020; Xi et al., 2025). For instance, Liu & He, (2022) showed that warming altered seedling mortality in a tropical forest by reshaping soil fungal communities, with reduced abundance of pathogenic fungi linked to lower mortality of *Ormosia semicastrata*. Huang et al. (2021) showed that warming increased mycorrhizal fungal

diversity while leaving pathogen diversity unchanged in a Tibetan meadow, to the benefit of some plant species and at the expense of others. Although some general trends in soil microbiome responses to climate change have been reported – e.g., increased bacterial: fungal ratios (Delgado-Baquerizo et al., 2020; Guerra et al., 2021) – the consequences for plant community composition are species-specific, determined by functional traits and co-evolutionary histories with soil microbes. It is clear from these studies that long-term predictions of community change must account for soil–climate–vegetation feedbacks.

Several key points emerge from these local-scale studies that have important implications for biodiversity conservation and policy. First, studying how plants respond to new (no-analog) climate-soil combinations is critical to predicting vegetation change under climate warming. Filling this knowledge gap will require a multi-pronged approach (as discussed above) to provide evidence-based guidance on when to expect ecological surprises (e.g., switches in species' positions on environmental gradients), when to anticipate rapid change or stability, and how to design adaptive interventions in the face of novel ecosystems. A second lesson is that we might expect relatively muted responses to climate where plants have evolved tolerance to stressful soil habitats (e.g., on serpentine soils) (Figure 1D), although this hypothesis requires testing in a broader range of soil contexts, such as karst soils or acidic wetlands. The results have important conservation implications, given that plant communities on stressful soils often contain multiple rare species (edaphic specialists) (Cartwright, 2019). Finally, given the influence of soil on microclimates, high local soil heterogeneity might buffer against the effects of climate change. For conservation purposes, areas of high edaphic heterogeneity can serve as local refugia, buffering broader communities against rapid climate-driven shifts.

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3. Soil effects on biogeographic plant migration

Across localities, climate warming is expected to prompt the "migration" of plants from lower to higher latitudes or elevations. Such range shifts are implicit in scenarios in Figure 1 where some species' niches overlap with future (red) but not current (blue) conditions, although studies of range shifts and of local community change are mostly done in isolation.

Predictions of plant migration largely rely on species distribution models (SDMs) – a group of statistical models that link species spatial distributions with environmental factors – which in the past most often overlooked soil properties (e.g., Dyderski et al., 2018; Thuiller et al., 2011). If climate and soil conditions are spatially correlated, assuming that species' range limits are controlled by climate alone could lead to erroneous conclusions. Climate-soil correlations indicate that if plants "follow" a set of climate conditions to higher latitudes or elevations, they will encounter different soils when they get there (e.g., Figure 2). If species are adapted to their current soils, unsuitable soils at higher latitudes could impede migration. In addition, if range limits are determined largely by soil, species' persistence might not depend on migration to the degree predicted by climate-only models. Here we discuss evidence, from both modeling and experimental studies, for the influence of soil properties on plant species' distributions, and how soil may affect migration under climate change.

3.1 Soil effects on current plant distributions

Although most SDMs are based on climatic predictors, some recent studies have found important roles of soil properties in explaining plant species' spatial distributions (summarized in Table S1, Supporting information). These studies show that key soil properties such as pH, moisture, and nutrient availability explain substantial variation in plant distributions at landscape to regional

scales; in some cases, soil factors are even more influential than climate, especially when predictions also include plant growth or abundance (e.g., Walthert et al., 2013; Walthert & Meier, 2017). For example, in an SDM for the occurrence of *Quercus pubescens* in France, adding soil pH improved model accuracy by about 30% (Bertrand et al., 2012). In models for >1800 plant species in eastern North America, soil variables were of comparable relative importance as climate variables (Ni & Vellend, 2024b). One potential statistical caveat is that if soil and climate variables are correlated (i.e., there is a collinearity problem), it can be difficult to disentangle their individual effects (Guisan et al., 2017; Ni & Vellend, 2024b); however, there is often sufficient independent variation to detect effects of both. Overall, incorporating soil variables into SDMs appears to improve the accuracy of distribution maps by capturing variation linked to edaphic heterogeneity, thereby providing a more realistic representation of current plant distributions.

Soil properties can also influence plants species' climate niches, and vice versa (Chapin, 1983; Hájek et al., 2021; Ingestad, 1979; Larcher, 2003; Lévesque et al., 2016). In other words, just as available soil and climate conditions can be correlated, so can soil and climate niches. For example, the thermal tolerance of *Q. pubescens* increases as a function of soil pH in temperate forests – possibly because greater nutrient availability in high-pH soils enhances physiological thermal tolerance (Bertrand et al., 2012). Along a mountain slope in eastern North America, soil pH and nutrients had stronger positive effects on understory herb occurrence and abundance at higher elevations (Ni & Vellend, 2024a), suggesting that plant persistence in colder environments might require higher soil moisture, nutrients or more suitable pH (Cross et al., 2015). Similar restrictions in soil niches under colder conditions were found across plant species in the European Alps (Chauvier et al., 2021). However, for bryophytes species in European fens,

soil niches were found to be more restricted (to higher pH) in warmer regions (Hájek et al., 2021). The general pattern appears to be that plants exhibit broader soil tolerances under their climatic optima, but narrower tolerances under suboptimal climates, although this hypothesis requires more comprehensive testing. Such interaction effects could increase the complexity of distribution modelling, while also underscore the point that omitting soils can lead to biased estimates of species' climatic niches.

The impact of soil on species' distributions is expected to vary depending on plant functional traits and habitat affiliations (Dubuis et al., 2012; Ni & Vellend, 2024b). Several preliminary studies have compared the importance of soil variables in SDMs across species. For example, two studies found that soil had weaker effects on the distributions of trees than of herbs and shrubs, possible due to deeper root systems of trees conferring greater resistance to soil stresses (Dubuis et al., 2012; Ni & Vellend, 2024b). Dubuis et al., (2012) also found that the influence of soil properties on spatial distributions increased as a function of a species' specific leaf area (SLA).

In addition to SDMs, field studies of species' range limits – both experimental and observational (Hargreaves et al., 2014) – have also demonstrated that soil properties, and soil-climate interactions can influence plant range limits along climatic gradients (Benning & Moeller, 2021b, 2021a; Bjorkman et al., 2017; Brown & Vellend, 2014; Collin et al., 2018; Ford & HilleRisLambers, 2020; Hagedorn et al., 2019; X. Lu et al., 2025; Solarik et al., 2019; Tourville et al., 2024). For *Clarkia xantiana* (an annual plant), whose distribution in southern California is strongly correlated with a precipitation gradient, fitness was greater when grown in within-range soil than in beyond-range soil in the field (Benning & Moeller, 2021b), likely due to higher water holding capacity and secondary nutrients (Ca, Mg, and S). Similarly, the growth

of experimental sugar maple (*Acer saccharum*) seedlings was reduced in soil from beyond vs. within the species elevational (climatic) range (Brown & Vellend, 2014), likely due to low soil cations (Carteron et al., 2020), and a lack of endomycorrhizal fungi (Carteron et al., 2020; Tourville et al., 2024). Moreover, poorly developed soils on bare ground on mountain tops can render high elevation sites unsuitable for species from lower elevations, independent of climatic conditions (Ford & HilleRisLambers, 2020).

Studies of elevation gradients and transplant experiments are particularly valuable for assessing soil effects along climatic gradients, as large-scale soil datasets are typically coarse and overlook fine-scale heterogeneity (Hengl et al., 2025). Intensive and strategic soil sampling can better capture soil variation and reduce collinearity between soil and climate predictors, while transplant experiments provide direct tests of whether range limits are constrained by climate, soils, or their interaction. In many contexts, we see that soil properties beyond species current range limits – along putatively climatic gradients – can constrain plant species' distributions (see Figure 3A).

Recent studies on trait—environment relationships and plant functional strategies have also advanced our understanding of plant adaptations along soil and climate gradients (Carmona et al., 2021; Carmona & Beccari, 2025; Cavender-Bares et al., 2016; Joswig et al., 2021; M. Lu et al., 2025; Ma et al., 2018; Tedersoo et al., 2020; Weigelt et al., 2021). For example, a global analysis of 17 plant traits (mostly leaf traits) showed that trait variation falls along two major axes: a size spectrum (e.g., plant height) driven by climate, and an economics spectrum (fast growth and turnover *vs.* slow growth and turnover) mediated by soil-climate interactions (Joswig et al., 2021). It was also found that traits related to soil resource acquisition and soil stress tolerance, such as specific root length and mycorrhizal associations, influenced the effect of soil

on plant distributions (Weigelt et al., 2021; Lu et al., 2025; Ma et al., 2018). For example, for European plants, facultatively and flexibly mycorrhizal species have the widest soil niches compared to non-mycorrhizal and obligately mycorrhizal plants (Gerz et al., 2018). Such advances in understanding links between plant traits and their responses to soil could greatly improve our ability to model plant migration along climatic gradients (Ovaskainen & Abrego, 2020; Peng et al., 2025), providing predictions, for example, of which temperate species might successfully colonize the nutrient-poor soils of boreal or tundra regions (see the discussion in next section).

3.2 Soil effects on historical and future plant migration

Changing availabilities of environmental conditions, soil-climate niches (Figure 1), and strong effects of soil in determining current plant distributions along climatic gradients (Figure 3A) point to important implications for plant migration under future climate change. However, just knowing that soil properties influence plant species' distributions does not tell us whether or how they will influence climate-driven migration specifically. There are four possible scenarios (Figure 3A):

Climate-dominated migration: With climate and soil uncorrelated, and species distributions limited by climate, plant migration should be little influenced by soil (Figure 3B), and therefore well characterized by a climate-only model.

Impeded migration: If soil suitability declines with latitude or elevation, migration should be impeded, relative to the climate-dominated scenario (Figure 3C).

Accelerated migration: If soil suitability increases with latitude or elevation, plant migration might occur even faster than predicted by a climate-only model (Figure 3D).

No migration: For species that mainly depend on soil and that are insensitive to climate, migration is not expected at all (not shown in Figure 3).

Studies from various perspectives, such as paleoecology, distribution modeling, and manipulative experiments, have begun to explore these scenarios. In a palaeoecological study, post-glacial tree migration appeared to have been slowed by a delay of 200-300 years between ice melt and sufficient soil development to support establishment (Pennington, 1986). Similarly, the late Holocene migration of Utah juniper (*Juniperus osteosperma*) appears to have been more constrained by soil than by climate – suitable soil patches for this species are small and spatially scattered, requiring a series of long-distance dispersal events (Lyford et al., 2003). These findings indicate that soil properties can slow plant migration (Figure 3C), particularly in polar regions where soils are poorly developed (e.g., thin and infertile soils) or unusually rich in organic matter (MacDonald et al., 2008; Svenning & Sandel, 2013). Interestingly, a recent vegetation resurvey study including 266 European forest understory species found that westward movements (over a period of decades) were 2.6 times more likely than poleward shifts; these shifts were mostly towards areas of high soil nitrogen deposition rather than newly suitable climates (Sanczuk, Verheyen, et al., 2024).

SDMs can be used to predict soil effects on potential plant migration by comparing the projections of climate-only models with projections of models incorporating soils (Table S1). For example, adding soil variables to a model with climate variables significantly increased predicted warming-driven range reduction for *Eucalyptus fastigata* in Australia (Austin & Niel, 2010). For plants in eastern North America, SDMs with only climate predictors substantially overestimated predicted poleward migration distances compared to climate-soil models, suggesting that high-latitude soils are generally unsuitable for plants from lower latitudes (Ni &

Vellend, 2024b). These studies point to potentially strong soil effects on future climate-driven migration, but they have a strong geographical bias – focusing on temperate regions. More soil-climate SDM studies are required for tropical ecosystems and drylands. In the case of migration from tropical to temperate zones, we would predict accelerated plant migration (Figure 3D), as temperate forest and grassland soils tend to be more fertile than tropical soils.

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SDM studies rely on existing soil maps, which are mostly of abiotic properties (Box 1), but soil biota can also have profound impacts on potential plant migration (Benning & Moeller, 2021a, 2021b; Fowler et al., 2023; Urli et al., 2016). Along climatic gradients (e.g., latitude, elevation), soil microbial communities can shift continuously, potentially slowing or accelerating migration (Tourville et al., 2024; Urli et al., 2016), much like physical or chemical soil properties (Figure 3). For example, Dalling & Willey (2025) noted that tropical lowlands are dominated by arbuscular mycorrhizal (AM) trees, whereas montane forests are dominated by ectomycorrhizal (ECM) Fagales, which leads to lower inorganic nitrogen and distinct inocula, creating unfavorable conditions for upslope establishment of AM species. Furthermore, Pither et al. (2018) showed that tree taxa associated with a greater diversity of ECM fungi migrated farther north during the last deglaciation, likely because richer ECM networks improved their tolerance of nutrient-poor northern soils. More broadly, species with wider edaphic tolerances may face weaker soil barriers and thus migrate faster, though this hypothesis remains untested. Mutualistic plant-fungi relationships are well studied but, plant-microbe interactions might also involve escape from species-specific pathogens beyond current range limits, thereby accelerating potential migration (Urli et al., 2016; Benning & Moller, 2021a).

Migration responses of soil mutualists and pathogens to climate warming might differ from that of plants, complicating predictions of their effects (Nuland et al., 2017, 2024; Ramirez et al.,

2019; Segal & Kivlin, 2025). For example, Nuland et al. (2024) predicted that climate change will reduce the overlap of suitable habitats between trees and their mycorrhizal partners for 35% of tree–ectomycorrhizal partnerships, especially at northern range limits, which may help explain the tree migration lag. With expanding regional- to continental-scale surveys of soil microbiomes – such as those conducted by the U.S. National Ecological Observatory Network (NEON) – it is becoming increasingly feasible to model the distribution dynamics of soil pathogens and mutualists (Luo et al., 2025; Nuland et al., 2024).

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To date, most SDMs are correlative, describing statistical associations between species occurrences and environmental predictors (Table S1). Mechanistic SDMs, by contrast, incorporate physiological limits, demographic rates, and dispersal processes, allowing them to capture key mechanisms underlying migration responses to climate change (Kearney & Porter, 2009; Sanczuk, Landuyt, et al., 2024; Zurell et al., 2016). Mechanistic SDMs are well suited for evaluating soil effects on migration, but this has been done in only a few studies (e.g., Liang et al., 2017; Meersch et al., 2025; Zani et al., 2022). For instance, using two mechanistic SDMs (PHENOFIT and CASTANEA) that explicitly model environmental effects on plant fitness and phenology, Meersch et al., (2025) showed that adding soil pH and water-holding capacity substantially improved reconstruction of post-glacial plant migration trajectories, particularly under non-analog climates. Spatial edaphic heterogeneity highlights the importance of including dispersal in models of plant migration (Box 1). For example, even when boreal–arctic soils appear unsuitable for temperate species, scattered edaphically suitable soil patches may exist (e.g., Ni & Vellend, 2024a). Reaching such isolated patches often requires rare long-distance dispersal events.

Because functional traits mediate plant responses to soil and climate, integrating trait data into hierarchical multispecies models such as joint species-distribution models (JSDMs) can substantially improve estimates of species' niches (Abrego et al., 2025; Ovaskainen & Abrego, 2020; Peng et al., 2025). This is particularly true for rare species – such as many edaphic specialists (Cartwright, 2019; Corlett & Tomlinson, 2020) – that are hard to model with standard SDMs. Incorporating empirical trait–soil relationships into JSDMs remains a promising but still underdeveloped approach (but see Pollock et al., 2012).

Several challenges remain in climate-soil SDM studies: *i)* The extrapolation problem: As discussed already, climate change may create novel combinations of climate and soil conditions (non-analog environments, Figure 1A, Chevalier et al., 2024), necessitating highly uncertain extrapolation. Manipulative experiments and mechanistic models can be powerful tools to test extrapolation accuracy and improve predictions in non-analog environments (Meersch et al., 2025). *ii)* Soil data accuracy: Large-scale soil maps (e.g., SoilGrids, Hengl et al., 2018, 2025) rely heavily on interpolation from limited field data (especially for tropical regions), and there is a pressing need for better soil data globally. *iii)* Soil dynamics under climate change: While some soil properties are unlikely to change substantially in the short term (e.g., depth, texture, geological substrate), others may change more rapidly due to direct effects of climate or vegetation shifts (e.g., pH, nutrients, microbiomes). Models of vegetation-climate-soil feedbacks will be required to capture these dynamics, but the empirical basis for broad-scale analyses is thin at present (Hengl et al., 2025).

4. Concluding Remarks and Future Perspectives

Despite their profound impact on plant fitness and their high spatial heterogeneity, soils are often overlooked in studies of vegetation dynamics under climate change. While it is common

knowledge that plants are influenced by soils, it is not at all obvious exactly how soils will impact the responses of species' distributions and community properties to climate change. We have shown how multiple lines of evidence have begun to reveal such impacts. Local communities on unusual soils (e.g., serpentine) often show reduced sensitivity to climate change, high soil heterogeneity can buffer climate impacts, and shifts in plant-soil feedbacks can have substantial impacts on plant abundances. The generality of these findings will require further tests. At a biogeographic scale, latitudinal soil gradients can influence species range limits and alter plant migration patterns, sometimes impeding or accelerating migration beyond what climate-only models predict. Finally, soil and climate effects are not independent - soil properties can influence microclimate and species climate tolerances, and climate change can also alter soil properties and biota.

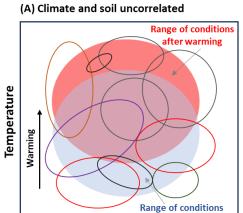
Our review underscores the importance of integrating soil properties into models predicting plant responses to climate change. Several predictions remain in need of further empirical testing, including two new predictions that emerged from our review (numbers 2 and 4):

- 1. Novel soil-climate combinations under climate warming are likely to generate plant communities with no modern analogs, distinct from today's assemblages.
- 2. There could be greater warming-driven species turnover when climate and soil gradients are correlated, given the great change of environmental space.
- 3. Soils with high mutualistic fungi diversity could buffer against climate change effects on plant communities.
- 4. Soil transitions from tropical to temperate regions could increase plant fitness for some species, potentially accelerating migration under climate change.

5. Spatial mismatches between plants and their mycorrhizal partners beyond current range limits could slow migration as climates warm.

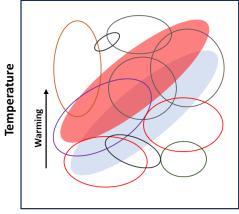
449 6. Species with broader edaphic tolerances may encounter weaker soil barriers and thus migrate450 more rapidly.

Overall, our synthesis shows that soils – through their physical, chemical, and biological dimensions – fundamentally reshape how plant communities and distribution ranges respond to climate change. Recognizing soil as a central axis of global change studies reveals both hidden constraints and overlooked opportunities for forecasting global vegetation futures. Integrating soils into experiments, monitoring networks, and next-generation mechanistic vegetation models and SDMs will be essential for anticipating novel ecosystems, identifying emerging refugia, and guiding proactive conservation strategies.



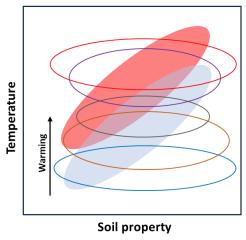


(B) Climate and soil correlated

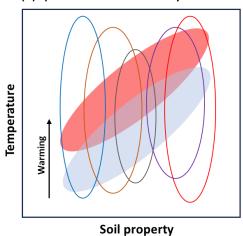


Soil property

(C) Species more constrained by climate



(D) Species more constrained by soil



(E) Reversal of species' positions on gradient

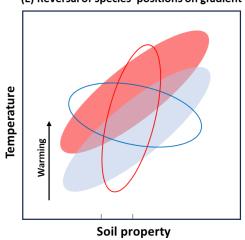


Figure 1. Conceptual illustration of how soil-climate environmental space and species' niches (in a hypothetical regional pool) influence plant responses to climate change. The blue and red solid ellipses represent current and future (under climate warming) environmental spaces, respectively. The hollow ellipses represent the fundamental niches of individual species — different colored ellipses represent different species. Black arrows show the direction of climate warming. (A) If climate is not correlated with soil, the new environmental space under climate warming still includes the environmental niches of many species. (B) If climate and soil are correlated, climate warming may create new environmental space largely outside of many species' niches. (C) If climate is the major constraint on plant distributions (narrow climate niches), community composition shows large changes. (D) If soil properties are the major constraint on plant distributions (narrow soil niches), community composition changes little. (E) Soil can prompt the reversal of species' positions along a climate-soil gradient.

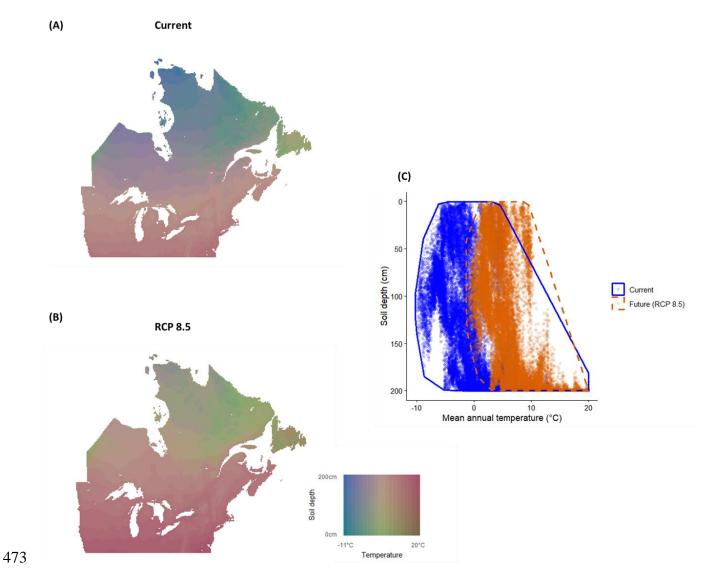


Figure 2. Climate (mean annual temperature) and soil depth in northeastern North America, illustrating how climate warming may generate novel soil—climate combinations. Currently, high-latitude regions are characterized by low temperatures and shallow soils (A), but future warming is expected to produce combinations of moderate temperatures with shallow soils (B), which do not exist in the current landscape. Panel (C) plots the current (blue) and future (orange) environmental space of temperature—soil depth combinations, with points indicating the underlying grid-cell data and polygons outlining the occupied environmental ranges. Mean annual temperature (°C) was derived from ClimateNA (Wang et al., 2016), and soil depth (cm, capped at 200 cm) from SoilGrids (Hengl et al., 2017). The RCP 8.5 scenario represents projected conditions under high CO₂ emissions by the end of this century (Meinshausen et al., 2011).

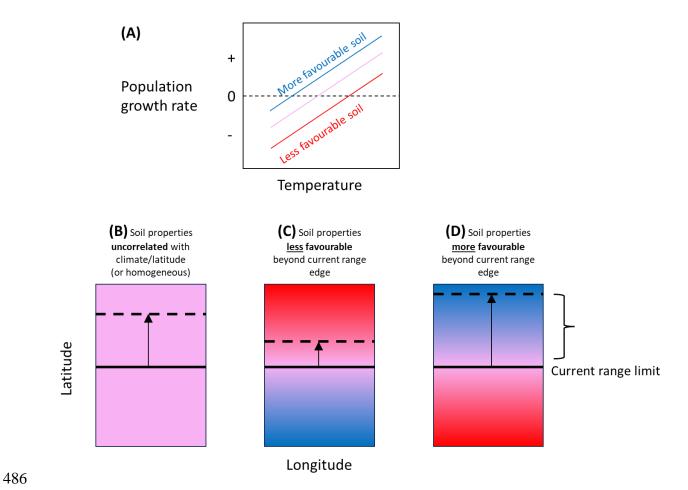


Figure 3. Qualitative predictions of plant migration with climate change in scenarios where population growth is determined by both climate and soil (A), and where the two are uncorrelated spatially (B), positively correlated (C), or negatively correlated (D). Scenarios assume a linear decrease of temperature with latitude, and an increase in temperature over time. Quantitative predictions would depend on the details of how population growth relates to temperature, and how temperature varies with latitude.

Box 1: Soil properties, spatial patterns, and mapping

Multiple soil properties can influence plant fitness (Larcher, 2003; Lévesque et al., 2016). Here we describe some key soil properties that could be important in modelling vegetation dynamics under climate change:

- 1. **Soil texture** refers to the proportions of different-sized solid particles (sand, silt and clay). Clay-rich soils typically hold more nutrients and water but have poor drainage compared to sandy soils.
- 2. **Soil nutrients** include macronutrients (N, P, K, etc.) and micronutrients (Fe, B, etc.), essential for plant tissue construction.
- 3. **Soil moisture** depends on precipitation and soil water holding capacity (itself determined by texture, organic matter, and other factors).
- 4. **Soil depth** influences plant root growth and the availability of water and nutrients. Deeper soils provide better access to water and nutrients, and greater potential for physical support.
- **5. Soil pH** is a function of the hydrogen ion concentration in the soil (-log₁₀[H⁺]). Soil pH is an indicator of multiple soil chemical properties (e.g., lower pH can lead to higher iron concentrations).
- **6.** The **soil microbiome** comprises highly diverse communities of bacteria, fungi (e.g., mycorrhizae), and archaea that drive nutrient cycling, organic matter decomposition, and plant—soil feedbacks.

Plant-relevant soil properties show high heterogeneity at all spatial scales, from local to continental (Bell et al., 1993; Weil & Brady, 2013). Over small distances (centimeters) soil properties can vary due to biotic activities (Xia et al., 2015), such as the enrichment of rhizosphere soil by root exudates (Robertson & Gross, 1994). At landscape scales, topography is crucial in regulating weathering (Ceddia et al., 2009). Regionally, soil patterns are driven by variation in parent material, climate, and vegetation. Consequently, many soil properties show a pattern of nested heterogeneity across space – gradually changing, continuous soil gradients at large scales with many small and discontinuous patches at small scales (Ettema & Wardle, 2002; Jr. et al., 2007; Woodruff et al., 2009). Such a nested pattern may play an important role in determining plant distributions and migration trajectories via highly patchy and fragmented suitable microsites.

Advances in global soil mapping have increased the feasibility of incorporating soils into vegetation modeling. The SoilGrids database (Hengl et al., 2017) offers global predictions of key soil variables (e.g., pH, texture) at 250m resolution. The new OpenLandMap–SoilDB extends this framework to 30 m resolution and tracks soil property dynamics over the past two decades (Hengl et al., 2025). The Harmonized World Soil Database (HWSD) and the Soil and Terrain Database (SOTER) offer regional-to-global coverage suitable for coarser-scale analyses. Some regional soil databases, such as the Soil Survey Geographic Database (SSURGO) for the USA, provide high-resolution soil profile and classification data. By combining regional soil surveys with advanced interpolation techniques (e.g., machine-learning methods), it is also possible to estimate soil properties independently for specific regions. However, fine-scale heterogeneity (e.g., a few meters) is unlikely to every be captured in broad-scale regional or global soil maps.

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