

Soil properties constrain predicted poleward migration of plants under climate change

Ming Ni  and Mark Vellend 

Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, J1K 2R1, Canada

Author for correspondence:

Ming Ni

Email: ming.ni@usherbrooke.ca

Received: 15 April 2023

Accepted: 5 July 2023

New Phytologist (2023)

doi: 10.1111/nph.19164

Key words: climate warming, continent, migration, plants, soil, species distribution models.

Summary

- Many plant species are predicted to migrate poleward in response to climate change. Species distribution models (SDMs) have been widely used to quantify future suitable habitats, but they often neglect soil properties, despite the importance of soil for plant fitness. As soil properties often change along latitudinal gradients, higher-latitude soils might be more or less suitable than average conditions within the current ranges of species, thereby accelerating or slowing potential poleward migration.
- In this study, we built three SDMs – one with only climate predictors, one with only soil predictors, and one with both – for each of 1870 plant species in Eastern North America, in order to investigate the relative importance of soil properties in determining plant distributions and poleward shifts under climate change.
- While climate variables were the most important predictors, soil properties also had a substantial influence on continental-scale plant distributions. Under future climate scenarios, models including soil predicted much smaller northward shifts in distributions than climate-only models (c. 40% reduction).
- Our findings strongly suggest that high-latitude soils are likely to impede ongoing plant migration, and they highlight the necessity of incorporating soil properties into models and predictions for plant distributions and migration under environmental change.

Introduction

Climate warming is expected to prompt the migration of many plant species to more poleward latitudes (Corlett & Westcott, 2013). Species distribution models (SDMs) are widely used to assess future suitable habitats (e.g. Thuiller, 2007; Thuiller *et al.*, 2011; Guisan *et al.*, 2017), but relatively few SDM studies have incorporated soil properties (e.g. Iverson *et al.*, 2008; Bertrand *et al.*, 2012; Beauregard & de Blois, 2014; Walthert & Meier, 2017), despite major effects of soil on plant performance (Larcher, 2003). Because soil properties can change substantially with latitude (Fig. 1; Hengl *et al.*, 2017), soil properties may play an important role in determining plant distributions at large spatial scales (regions to continents), constraining plant latitudinal ranges. Assuming that climate warming shifts suitable climatic conditions poleward, then if soil conditions beyond previous climatically determined range limits are more suitable than average conditions within the range, range shifts ('migration') might occur faster than predicted by a climate-only model. By contrast, if soil conditions beyond the range are relatively unsuitable, poleward migration would be impeded. However, these possibilities have been rarely tested in predictive models (Laffleur *et al.*, 2010; Bertrand *et al.*, 2012). SDMs neglecting soils might thus misrepresent species–environment relationships and therefore projections of future suitable habitats (Bertrand *et al.*, 2012).

It has been claimed that soil properties are unlikely to influence plant distributions across continents, given that they vary more at fine than broad spatial scales (Siefert *et al.*, 2012). However, the major influences on soil – geology, climate, and vegetation, age – can vary greatly at continental scales (Weil & Brady, 2013), so this assumption seems unlikely to hold in general. In Eastern North America (ENA), cold and young postglacial soils at high latitudes lead to shallow, water-logged conditions (Cryosols), or humid, acidic, nutrient-poor conditions (Podzols). By contrast, soils in more southerly temperate forests are more fertile with higher pH (Luvisols; Weil & Brady, 2013). Globally, soil microbial diversity and composition also vary across latitudes (Bahram *et al.*, 2018). Thus, soil properties change greatly with latitude (Fig. 1) and may have a major influence on continental plant distributions. Some recent SDM studies have found significant effects of soil properties on plant distributions (e.g. Bertrand *et al.*, 2012; Beauregard & de Blois, 2014; Walthert & Meier, 2017), although spatial extent of these studies was defined largely by political borders (e.g. Switzerland, France, and Quebec) with a focus on temperate forests. Given that climate warming can induce migration across biomes at the continental scale (Lenoir & Svenning, 2014), predicting future distributions will require quantitatively evaluating the relative importance of soil and climate properties at larger spatial scales across multiple biomes.

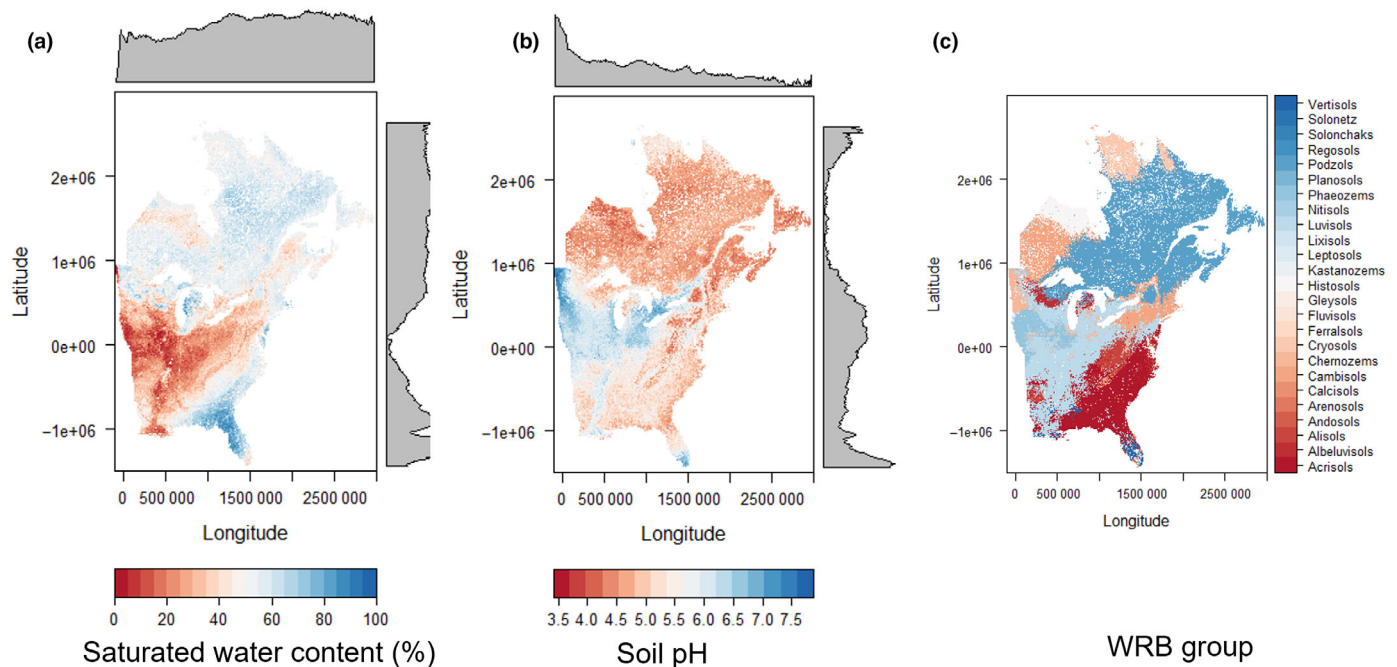


Fig. 1 Spatial pattern of three key soil properties in eastern North America (a–c). Marginal plots summarize the mean values across latitudes and longitudes. WRB, World Reference Base for Soil Resources.

Potential plant migration could be strongly impacted if sites that become climatically suitable have unsuitable soil (Lafleur *et al.*, 2010; Brown & Vellend, 2014; Carteron *et al.*, 2020; Greiser *et al.*, 2020; Benning & Moeller, 2021a,b). If so, apparent migration lags (Fei *et al.*, 2017; Talluto *et al.*, 2017; Boisvert-Marsh *et al.*, 2019) might be due in part to overestimates of how far suitable growing conditions have shifted. Potential future species richness in poleward sites might also be overestimated by climate-only models. The most direct model-based test of this idea would be to quantitatively compare projections of climate-only models and climate+soil models, across many species, at a continental scale. To our knowledge, only one study has conducted such a model comparison: Bertrand *et al.* (2012) compared range shift projections for a single species (*Quercus pubescens*) in temperate forests of France, finding that the future range limit of *Q. pubescens* projected in a climate+soil model was further north than that in a climate-only model. This study did not involve a major latitudinal gradient in soil properties across biomes, and the generality of this conclusion is unknown.

To the extent that soil properties influence plant distributions, we might expect their relative influence to depend on species growth forms and habitat types. Tree species generally possess deeper and larger root systems than shrubs and herbaceous plants, potentially reducing any influence of soil properties (Beauregard & de Blois, 2014). Wetlands generally have unique soil environments – high organic matter content and waterlogging, and thus, wetland plants may have more restricted soil requirements than species from other habitats (such as forests). This hypothesis has not been tested across multiple species at a continental scale (Michaelis *et al.*, 2016).

Here, we investigate how soil properties (fine resolution, 250 m × 250 m) influence the current distributions and the projected poleward migration of 1870 plant species across ENA. We predicted that: soil properties play an important role in explaining current species distributions at a continental scale; climate+soil models generally project smaller northward shifts in suitable habitats and lower potential species richness in poleward sites than climate-only models, given relatively unsuitable soils at high latitudes in this region; the relative importance of soil properties depends on growth forms (greater for herbs and shrubs than trees) and habitat types (greater for wetland species than for others).

Materials and Methods

Methods overview

We first built three SDMs for each of 1870 plant species native to Eastern North America (ENA): one SDM trained with three climate predictors ($SDM_{climate}$; variable selection described later); one SDM trained with eight soil predictors (SDM_{soil}); and one trained with the same three climate predictors, plus the eight soil predictors (SDM_{sc}). We then calculated the relative importance value of each predictor in SDM_{sc} to evaluate the contributions of soil and climate to explaining current species distributions (Hypothesis 1). We also partitioned the variation attributable to unique or joint effects of climate and soil predictors; given that both climate and soil are correlated with latitude (the motivation of our study), we expect considerable shared variation, but imperfect correlations should also provide scope for detecting unique effects. For Hypothesis 2, we used SDM_{sc} and

SDM_{climate} to project species' suitable habitats under two future climate scenarios and then compared the difference in projected poleward shifts between SDM_{climate} and SDM_{sc}. We also compared projected patterns of species richness (summing up the habitat suitability of each species in each grid cell) between the two models. We compared predictor-variable importance values among plant growth forms and among habitat types to test Hypothesis 3.

Species and environmental data

Species occurrence data were obtained from the Botanical Information and Ecology Network (BIEN; Enquist *et al.*, 2016), which is one of the largest plant distribution datasets for North America, including plant records from multiple data sources (e.g. many herbaria and the Global Biodiversity Information Facility, GBIF). The database includes 2408 terrestrial vascular plant species native to ENA with > 50 occurrence records per species. Here, we defined the spatial extent of ENA to include the eastern states or provinces of the United States and Canada that are dominated by forest ecosystems rather than prairies (Fig. 1). We restricted analyses to ENA to focus on the north–south gradient of temperature and biomes (forests, wetland, and others) under relatively homogenous precipitation conditions, avoiding the water-stressed prairie biome to the west (future precipitation scenarios have far more uncertainty than future temperature scenarios; Woldemeskel *et al.*, 2012). ENA possesses a relatively coherent biogeographic flora, with many plant species having distributions almost entirely within this biogeographic region. We first downloaded all species occurrences in the Americas and calculated the proportion of their occurrences in ENA, excluding those species with more than half of their occurrences outside ENA. We retained 1870 species in our analyses, while also analyzing the subset of 1080 'endemic' species with > 90% of their occurrences in ENA. The species data were downloaded using the 'BIEN' package in R (Maitner *et al.*, 2018). We did not include naturalized alien species in this study, given a strong influence of human introduction and cultivation (Donaldson *et al.*, 2014).

For current and future climate across ENA, we used the ClimateNA program (Wang *et al.*, 2016) to extract all 27 climate variables available (Table A in Supporting Information Notes S1) with 250 m × 250 m resolution. The elevation data used for climate interpolations were from Multi-Error-Removed Improved-Terrain Digital Elevation Models (MERIT DEM; Hengl, 2018). Climate variables at the end of 21st century (2071–2100) were taken from projections using two emission scenarios: RCP4.5 for moderate glasshouse concentration and RCP8.5 for high glasshouse gas concentration, and each projection represented an ensemble of 13 common General Circulation Models (GCMs; Wang *et al.*, 2016). For soil, we first chose 18 soil variables (the full list provided in Table A, Notes S1) that could influence plant fitness from the Soilgrid database with 250 m × 250 m resolution (Hengl *et al.*, 2017). The soil data were interpolated based on data from multiple sources and so involve some uncertainties (see Hengl *et al.*, 2017 for the uncertainty of each variable). This spatial resolution is greatly improved compared with previous

studies: for example, 20 km × 20 km in Iverson *et al.* (2008), 55 km × 55 km in Morin & Lechowicz (2012), and 1 km × 1 km in Chauvier *et al.* (2021). It is closer to the spatial scale at which soils influence plant fitness. For variables reported at multiple soil depths (0–200 cm), we chose the 5 cm layer because plant roots are mainly distributed in surface soils (Schenk & Jackson, 2002; Luo *et al.*, 2021) and because of very strong correlations across depths. All the environmental data (and species distributions) were equal-area projected using the Lambert conformal conic projection. To reduce multicollinearity among the environmental variables included in models (all climate and soil variables), Pearson's correlations and variance inflation factors (VIF) were used for variable selection (i.e. Pearson's correlation < 0.7 and VIF < 10). In the final models, we kept eight soil variables (soil pH, coarse fragment content, absolute soil depth, soil depth to R horizon, cumulative Histosol content, saturated water content, sodic grade, and soil order) and three climate variables (mean annual temperature, mean annual relative humidity, and summer heat moisture index). The Pearson's correlations between selected variables are provided in Fig. A in Notes S1. Soil orders were from the World Reference Base (WRB) for Soil Resources.

Model calibration

Because BIEN only provides data on presences, we generated the same number of absences ('pseudo-absences') as there were presences for a given species, which Barbet-Massin *et al.* (2012) showed to be the best strategy for the three algorithms we chose (see next paragraph). The locations of pseudo-absences were chosen randomly within ENA. Using the 'SDM' package in R (Naimi & Araújo, 2016), we built three ensemble SDMs for each species: SDM_{sc}, containing both the eight soil variables and three climate variables as predictors; SDM_{soil}, containing only soil variables as predictors; and SDM_{climate}, containing only climate variables as predictors. Species presence/absence was the response variable.

The ensemble models included the three most common modelling algorithms: generalized additive models (GAM), boosted regression trees (BRT), and random forests (RF). Such ensemble models, averaging several algorithms, produce more robust forecasts than individual algorithms (Araújo & New, 2007). Models were calibrated using an 80% random sample of the dataset for each species and evaluated against the remaining 20% of data using true skill statistics (TSS), the area under the receiver operating characteristics curve (AUC), and pseudo- R^2 (Cohen's R^2 , based on model deviance). Higher values of these indices indicate higher predictive performance of models. This procedure was repeated five times to increase model robustness for each species.

Evaluating the importance of soil variables

We quantified the influence of soil properties on a given species distribution in three ways: the relative importance of soil properties in SDM_{sc}; the difference in model performance (TSS, pseudo- R^2 , or AUC) between SDM_{sc} and SDM_{climate}; and the proportion of variation uniquely attributable to soil in the full

model (see variation partitioning method described later). The relative importance of each variable was calculated as one minus the correlation between the prediction of the original model and the prediction of a model with the variable of interest randomized. These were first calculated for each predictor for each species using the 'getVarImp' function in the SDM package and then as the mean across all 1870 species. To evaluate the total influence of soil predictors vs climate predictors, we also calculated the sum of the relative importance values for the eight soil predictors (overall 'soil importance') and for the three climate predictors (overall 'climate importance'). For variation partitioning, we subtracted the pseudo- R^2 values of $SDM_{climate}$ and SDM_{soil} from the pseudo- R^2 of SDM_{sc} , yielding the partial variation uniquely explained by soil or climate predictors, respectively. Subtracting the sum of the two partial contributions from the pseudo- R^2 of SDM_{sc} yields the variation jointly explained by climate and soil (Zimmermann *et al.*, 2007).

To test Hypothesis 3, we compared the importance of soil and climate variables among four major plant functional groups – trees, shrubs, herbs, and climbers (vines and lianas). Growth form data were extracted from BIEN, Flora of North America (Flora of North America Editorial Committee, 1993) and the USDA Plants Database (USDA & NRCS, 2023). Because relative importance values ranged from 0 to 1 (not normally distributed), we used pairwise Wilcoxon rank-sum tests to test for significant differences among functional groups. The same procedure was used to compare species in three habitat groups: wetlands, forests, and other habitats. Information on species habitats was obtained from Gleason and Cronquist (1991) and Flora of North America Editorial Committee (1993), which together provided habitat information for 1725 of our species (the rest were excluded from this analysis). We chose three habitat groupings (instead of finer divisions) as a way to minimize uncertainty in classification and to maximize intergroup interpretability and intragroup sample size. 'Wetland' species included those described as occurring in marshes, river banks, fens, wet ditches, pond margins, bogs, lakeshores, shorelines, boggy/moist/wet/peaty meadows, mud, swales, wet places, pocosins, etc. 'Forest' species were described as occurring in forests, woods, or woodlands that are dry, moist, wet, open, rich, rocky, upland, mesic, coniferous, boreal, or deciduous, in addition to hammocks, pine barrens, and related terms. Our third category 'other' included species occurring in any other habitat type (e.g. grassland, and openland, which are not natural habitats in most of ENA, and where species are mostly generalists occurring in multiple habitats) or in multiple habitat types. There were too few species in more subdivided categories for meaningful analysis.

To assess the potential need to control for phylogenetic relatedness among species, we tested the phylogenetic conservatism of soil/climate importance (mentioned previously) using Blomberg's K test (Blomberg *et al.*, 2003). Specifically, we used the V.PHYLOMAKER (Jin & Qian, 2019) package in R to build a phylogenetic tree of 1076 plant species (details in Notes S2) and then calculated Blomberg's K for each variable. We found no evidence of phylogenetic conservatism for either soil or climate importance, so no corrections were applied to our models making interspecific comparisons.

Model projections for current and future suitable habitats

Habitat projections only involved SDM_{sc} and $SDM_{climate}$, but not SDM_{soil} because there are no projections of future soil conditions. All calibrated SDM_{sc} and $SDM_{climate}$ were projected under current and two future climate conditions (RCP4.5 and RCP8.5) at a 250 m × 250 m resolution. The projected habitat suitability from the three modelling algorithms and five repetitions were weighted by their TSS in the final ensemble. We classified projected habitat suitability (0–1) into binary habitat maps using the threshold that maximizes model TSS. For each species in each RCP scenario, we then calculated the area (km²), mean latitude, and 95th percentile of latitude (northern range limit) of suitable habitat projections.

To assess the influence of soil properties on the area and latitudinal distributions of suitable habitats, we compared SDM_{sc} and $SDM_{climate}$ projections in two ways. First, we compared the areas (km²) and latitudinal distributions of suitable habitats across all species between SDM_{sc} and $SDM_{climate}$ under each climate scenario. Second, we calculated the differences in mean and 95th percentile of latitudes of suitable habitats between current and future climate scenarios (RCP4.5 and RCP8.5, respectively); these represent predicted poleward shifts of suitable habitats for each species. Then, we compared the predicted poleward shift of suitable habitats between SDM_{sc} and $SDM_{climate}$ across all species to evaluate the possible effects of soil properties on plant migration.

Although it has been documented that incorporating soil variables into SDMs can lead to increases in projected range shifts (Bertrand *et al.*, 2012), there is nonetheless some concern that adding environmental variables will have a statistical tendency to project smaller ranges – adding environmental constraints can reduce species' suitable habitats, potentially leading to fewer suitable habitats at both range limits and so narrower distribution ranges (similar to the sampling effect in Ni and Vellend, 2021). A purely statistical effect would apply to both northern and southern range limits, so to explore this possibility we also compared the full latitudinal ranges of predicted suitable habitats, calculated as the 95th percentile latitudes minus 5th percentile latitude, under future climate scenarios between SDM_{sc} and $SDM_{climate}$. If SDM_{sc} does not project smaller latitudinal ranges than $SDM_{climate}$, it means that adding environmental constraints does not necessarily project smaller distribution ranges. Two-tailed t -tests were used to assess statistical significance for each comparison. We also mapped species richness by summing the habitat suitability across all 1870 species for each 250 m × 250 m grid cell under each climate condition. We calculated the difference in richness predicted by SDM_{sc} and $SDM_{climate}$ to assess possible soil effects on future plant richness.

Analyses of endemic species

Because some of our selected species are not endemic to ENA (with 0–50% occurrences outside ENA), SDMs might truncate their estimated niches. Thus, we tested the robustness of our major conclusions by also conducting key analyses for endemic

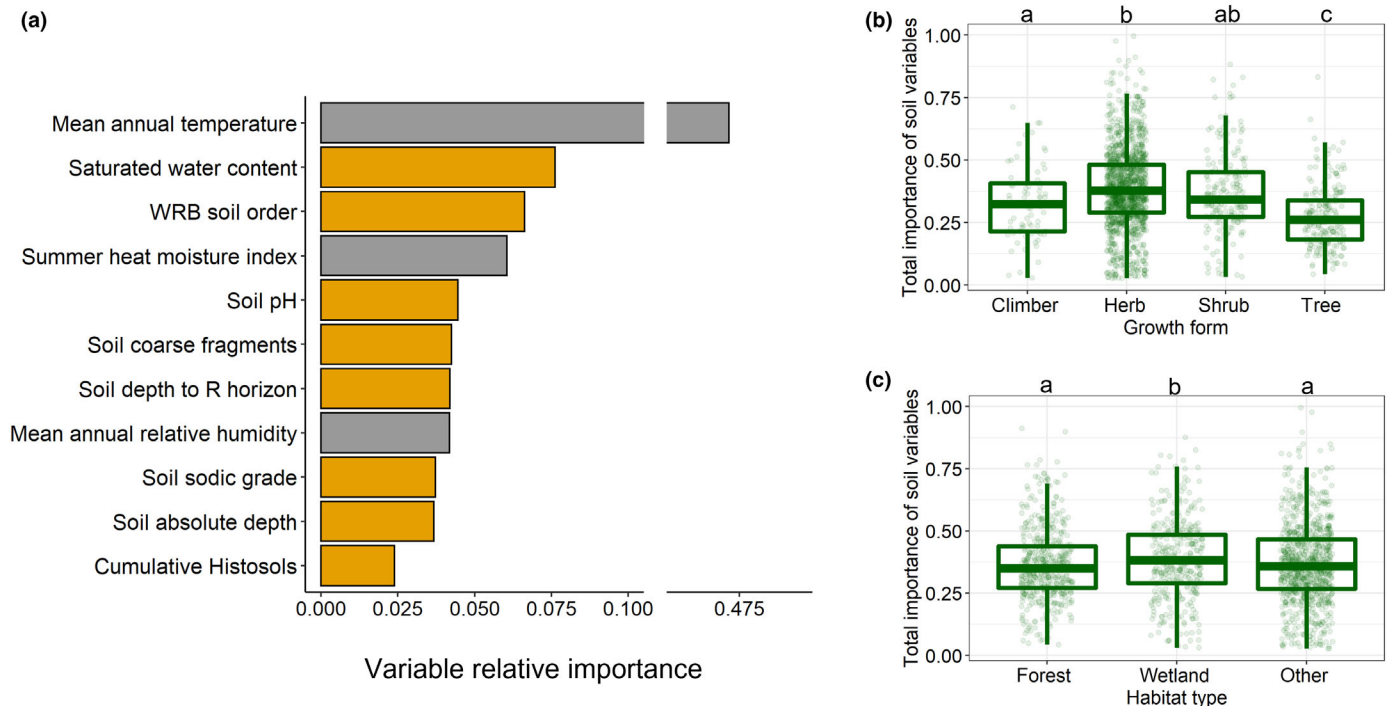


Fig. 2 Relative importance of climate and soil variables in predicting species distributions. (a) The mean relative importance value across species (x-axis) of eight soil variables (orange bars) and three climate variables (grey bars) in the model with both climate and soil variables (SDM_{sc}). (b, c) The summed relative importance of soil variables among plants of different growth form (b) and habitat affinity (c). Annotations (a–d) on the top of (b, c) indicate pairwise comparisons between groups, with different letters indicating significant differences ($P < 0.05$). The lower and upper hinges of box plots correspond to the 25th and 75th percentiles, and the lower/upper whisker extends from the hinge to the smallest/largest value no further than $1.5 \times IQR$ (interquartile range: the distance between the first and third quartiles) from the hinge. SDM, species distribution model; WRB, World Reference Base for Soil Resources.

species only (here defined as $\geq 90\%$ occurrences in ENA, 1080 endemic species in total). These analyses focused on comparisons of model performance between SDM_{sc} and $SDM_{climate}$, the mean relative importance values of different variables, and predicted shifts in latitudes between SDM_{sc} and $SDM_{climate}$ under different climate scenarios.

All statistical tests were conducted in R 4.0.3 (R Core Team, 2020). The SDM calibration, projection, and the calculation of variable relative importance were conducted using the ‘SDM’ package (Naimi & Araújo, 2016) in R.

Results

Soil effects on species distributions

The summed relative importance of the eight soil predictors and the three climate predictors were, on average (across species), 0.369 and 0.573, respectively. The most important climate predictor, and the most important predictor overall, was mean annual temperature (mean relative importance = 0.471), while the next two most important were soil variables: soil saturated water content (mean relative importance = 0.0762) and soil order (0.0662; Fig. 2a). Saturated water content represents the ability of soils to hold moisture, thus having a major influence on soil moisture; WRB soil order is a synthetic categorical variable related to soil texture, acidity, and nutrient content, all of which

are important to plant fitness. Soil pH was the third most important soil predictor – suitable soil pH is necessary to maintain root physiological activities for plants. Soil absolute depth and cumulative histosols (soils that are composed mainly of organic materials) overall had the least influence on species’ distributions (Fig. 2a).

The relative importance of soil predictors was significantly higher for herbs and shrubs than for trees ($P < 0.01$; Fig. 2b), and climbers were less influenced by soils compared with herbs; the relative importance of climate predictors showed the opposite trend among growth forms (Fig. D in Notes S3). Soil predictors were significantly more important for species of wetland habitats than for forest species or species in other habitats (Fig. 2c); climate variables were of similar importance for species in the three habitat groups (Fig. D in Notes S3).

On their own, soil and climate variables were of comparable importance in explaining distributions, with the climate models somewhat better; the climate + soil models performed best. Across the 1870 species, SDM_{soil} had an average TSS of 0.735 and an area-under-the-curve (AUC) of 0.903, and $SDM_{climate}$ had an average TSS of 0.759 and an AUC of 0.913, while the averages for SDM_{sc} were somewhat higher: 0.787 (TSS) and 0.927 (AUC). The difference between SDM_{sc} and $SDM_{climate}$ was significant for both TSS (Student’s *t*-tests: $t = 8.1307$, $P < 0.001$) and AUC ($t = 9.4292$, $P < 0.001$). Although the overall mean differences in TSS or AUC between $SDM_{climate}$ and

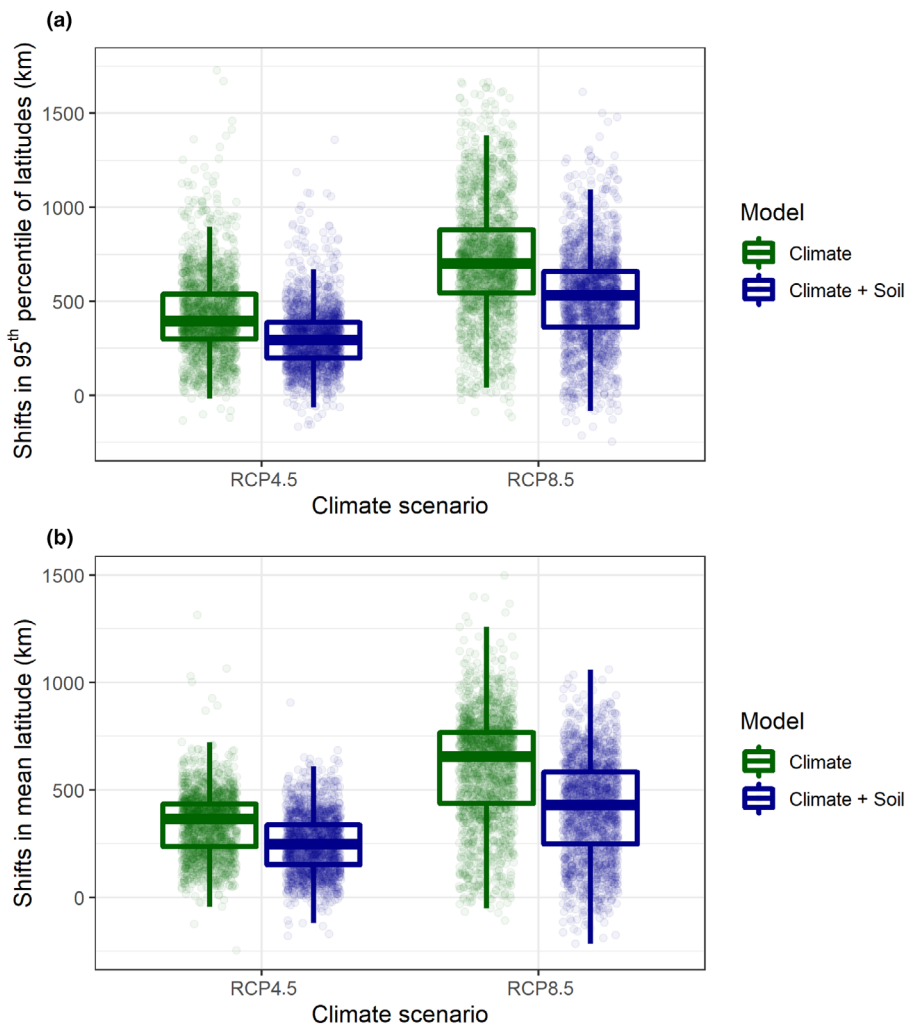


Fig. 3 Box plots showing predicted latitudinal shifts of suitable habitats from $\text{SDM}_{\text{climate}}$ (green) and SDM_{sc} (blue). (a) The predicted difference of mean latitude between current and future climate scenarios (RCP4.5/RCP8.5) across species. (b) The predicted difference in the 95th percentile of latitudes of suitable habitats between current and future climate scenarios (RCP4.5/RCP8.5) across species. The lower and upper hinges of box plots correspond to the 25th and 75th percentiles, and the lower/upper whisker extends from the hinge to the smallest/largest value no further than $1.5 \times \text{IQR}$ (interquartile range) from the hinge. SDM , species distribution model.

SDM_{sc} were small, soil variables increased TSS by > 0.1 for 159 species (Fig. E in Notes S4), and AUC by > 0.05 for 181 species (Fig. E in Notes S4). Average pseudo- R^2 was 0.539 for SDM_{soil} , 0.581 for $\text{SDM}_{\text{climate}}$, and 0.615 for the full model SDM_{sc} . The partial pseudo- R^2 for soil predictors alone was thus low (0.035, 6% of the full model), and for climate predictors, it was 0.076 (12% of the full model). Most of the variation (partial pseudo- $R^2 = 0.505$) was jointly explained by soil and climate predictors together (82% of the full model).

Projections of suitable habitats

$\text{SDM}_{\text{climate}}$ predicted significantly larger northward shifts of suitable habitats, with respect to both mean latitudes (Fig. 3a) and northern range limits (95th percentile of latitudes; Fig. 3b) than SDM_{sc} under both climate scenarios. Specifically, $\text{SDM}_{\text{climate}}$ predicted on average 41% more change in 95th percentile latitudes than SDM_{sc} under RCP4.5, and 40% under RCP8.5 (Fig. 3b). For mean latitude, the differences were 38% for RCP4.5 and 45% for RCP8.5 (Fig. 3a). Out of the 1870 species, 1398 (75%) showed smaller predicted northward shifts (95th percentile latitudes) under RCP4.5 when adding soil properties into

models; this was the case for 1437 species (77%) under RCP8.5 (Fig. F in Notes S4). Similar trends were found for mean latitudes (Fig. F in Notes S4). Fig. 4 (Fig. G in Notes S4) illustrates the results for one species, *Erythronium americanum*, for which $\text{SDM}_{\text{climate}}$ predicted substantially greater northward shifts in suitable habitats than SDM_{sc} under future climate scenarios.

Compared with $\text{SDM}_{\text{climate}}$, SDM_{sc} predicted similar current latitudinal distributions under current climates but different distributions under future climates. Specifically, for the current climate scenario, SDM_{sc} and $\text{SDM}_{\text{climate}}$ predicted similar northern range limits (95th percentile of latitudes) for suitable habitats across species ($t = -0.611$, $P = 0.5412$) the same was true for mean latitudes ($t = 0.122$, $P = 0.903$). For the future scenario RCP4.5, $\text{SDM}_{\text{climate}}$ predicted significantly higher values than SDM_{sc} for both 95th percentile latitude ($t = 4.503$, $P < 0.0001$; Fig. H in Notes S4), and mean latitude ($t = 4.488$, $P < 0.0001$; Fig. H in Notes S4). Similar differences were found for RCP8.5 (95th percentile of latitudes: $t = 7.663$, $P < 0.0001$; mean latitude: $t = 8.1944$, $P < 0.0001$). However, adding soil to SDMs does not necessarily cause smaller predicted ranges overall. SDM_{sc} and $\text{SDM}_{\text{climate}}$ projected similar values of future latitudinal ranges (95th – 5th percentile latitudes) under both future

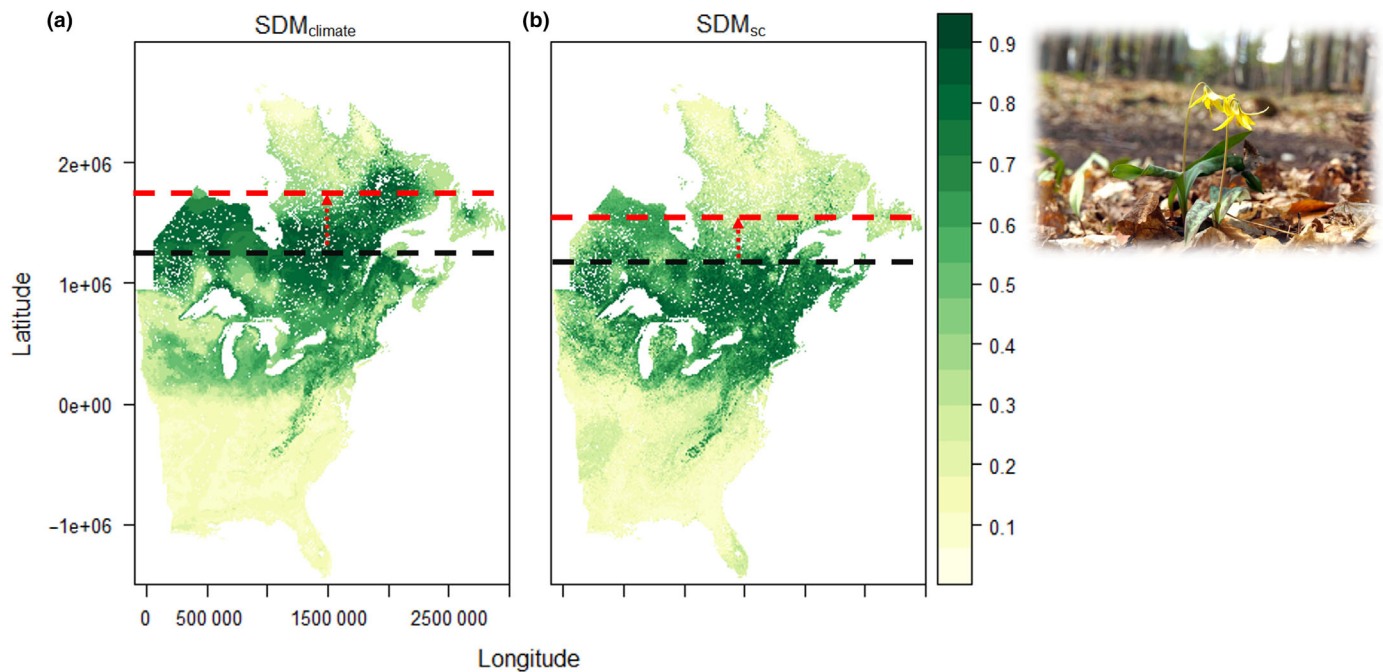


Fig. 4 Future habitat suitability projected for *Erythronium americanum* by $SDM_{climate}$ (a) and SDM_{sc} (b), under climate change scenario RCP8.5. Map color represents predicted habitat suitability under climate change. Black dashed lines show the northern range limits (95th percentile latitude) of suitable habitats under current climate, and red dashed lines show the northern range limits of suitable habitats under the future climate scenario. Red arrows show the predicted poleward shifts of suitable habitats. Results for RCP4.5 are shown Fig. G in Supporting Information Notes S4. The photo shows *E. americanum* in Parc national du Mont Mégantique, Québec. SDM, species distribution model.

climate scenarios (RCP4.5, $t=0.4575$, $P=0.6473$; RCP8.5, $t=1.2126$, $P=0.2254$), and $SDM_{climate}$ even predicted smaller latitudinal ranges than SDM_{sc} under current climate ($t=-10.719$, $P<0.001$).

For the total area of suitable habitat (potential range size), $SDM_{climate}$ predicted significantly larger areas than SDM_{sc} under all climate conditions (current, RCP4.5 and RCP8.5; Fig. I in Notes S4; $P<0.0001$ under all Student's t -tests). For species richness, both SDM_{sc} and $SDM_{climate}$ predicted increases in potential plant species richness at high latitudes (e.g. Great Lakes Region) and decreased richness at low latitudes (e.g. Florida) under future climate scenarios (Figs J, K in Notes S4). SDM_{sc} predicted lower future plant richness than $SDM_{climate}$ in northern Quebec, but higher richness in the Great Lakes and Appalachian regions under future climates (RCP4.5 and RCP8.5; Fig. 5).

Endemic species

For the 1080 endemic plant species (>90% occurrences in ENA), the major results were similar to those for the full set of species (Notes S5). Specifically, SDM_{sc} overall had better performance than $SDM_{climate}$, according to both AUC and TSS ($P<0.001$ for both t -tests; Fig. L in Notes S5). The summed relative importance of the eight soil predictors and the three climate predictors were, on average (across species), 0.363 and 0.557, respectively (Fig. M in Notes S5). The most important predictor overall was mean annual temperature (mean relative importance = 0.463), while the next two most important were

soil variables: soil saturated water content (mean relative importance = 0.0782) and WRB soil order (0.0761; Fig. M in Notes S5). For species' future suitable habitats, $SDM_{climate}$ predicted significantly higher northward shifts (mean latitudes and 95th percentile of latitudes; Fig. N in Notes S5) than SDM_{sc} under both climate scenarios. Specifically, SDM_{sc} predicted on average 53.5% less change in 95th percentile latitudes than $SDM_{climate}$ under RCP4.5, and 47.6% under RCP8.5 (Fig. N-a in Notes S5). For mean latitude, the differences were 40.5% for RCP4.5 and 51.7% for RCP8.5 (Fig. N-b in Notes S5).

Discussion

Our results support the hypothesis that soil properties can play an important role in determining plant distributions at a continental scale. Although the proportion of variation attributed uniquely to soil was small, likely due to correlated climate and soil gradients, adding soil variables to SDMs nonetheless had a major impact on predicted potential future distributions. This suggests that higher-latitude soils in our study region are relatively unsuitable for many species that otherwise might be expected to migrate from lower latitudes due to climate warming. To our knowledge, this is the first model-based demonstration that incorporating soil variables greatly reduces the magnitude of predicted poleward shifts in suitable habitat under climate change for many species at a continental scale. In addition, the importance of soil properties varied predictably among species of different growth forms and habitat types, with stronger effects for

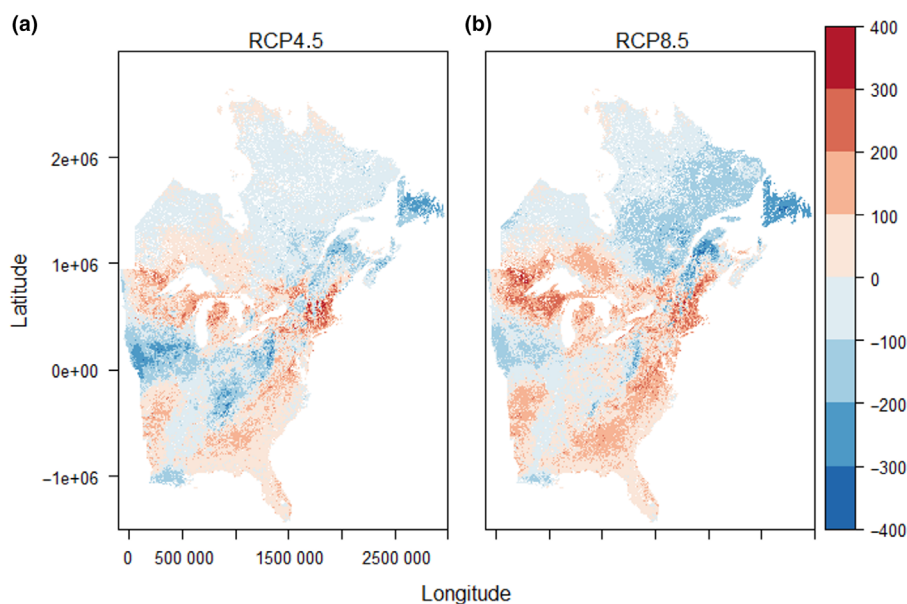


Fig. 5 Differences in projected richness between SDM_{sc} and $SDM_{climate}$ ($SDM_{sc} - SDM_{climate}$) under future climate scenarios RCP4.5 (a) and RCP8.5 (b). SDM, species distribution model.

shrubs and herbs than for trees and climbers, and stronger effects for wetland species compared with species of forests and other habitats.

While climate variables were the best predictors of species' distributions (mean relative importance = 0.573), soil variables (mean relative importance = 0.369) had major impacts as well, explaining a considerable proportion of spatial variation in species occurrences. The three most important soil predictors were saturated water content, WRB soil order and pH (Fig. 2a), which are all important for plant fitness (Larcher, 2003) and vary substantially across latitudes (Fig. 1). While some soil properties had minimal explanatory power for current distributions, they might nonetheless influence species' migration under climate change. For example, soil depth generally was of minor importance in SDM_{sc} (Fig. 2a) – possibly because data limitations show little variation across most of ENA except at high latitudes. However, widespread shallow soils and rock outcrops in northern areas might not be suitable for many species migrating from the south in the coming decades (Lafleur *et al.*, 2010; Ford & HilleRisLambers, 2020).

Although soil predictors did not result in large improvements in model accuracy, correlations between soil and climate variables in our data make it difficult to precisely assign unique variation to climate vs soil. That is, climate predictors alone might capture some spatial variation in species occurrences that is driven by soil, and vice versa (Guisan *et al.*, 2017). The results of variation partitioning suggest that most variation in species occurrence was jointly explained by soil and climate predictors, and SDM_{soil} had similar TSS or AUC as $SDM_{climate}$, which is consistent with previous findings at smaller scales, for example in analyses restricted to southern Quebec (Beaugard & de Blois, 2014) or the European Alps (Chauvier *et al.*, 2021). As such, our estimates of the additional contribution of soil variables (on top of climate) might be conservative. Regardless, we expect that including soil properties in SDMs will more accurately characterize

species–environment relationships and thus projections of potential future suitable habitats.

Our most novel result is that potential species distribution shifts under climate change were profoundly influenced by soil conditions, which have generally been neglected in previous predictions (e.g. Thuiller *et al.*, 2011; Dyderski *et al.*, 2018; Fricke *et al.*, 2022). In our study, including soil variables (SDM_{sc}) led to predictions of far smaller shifts (*c.* 40% reduction on average) in the latitudes of suitable habitats under different future climate scenarios (Fig. 3). We would thus predict that many species will have difficulty colonizing high-latitude sites beyond their current range limits, even if climatic conditions become suitable. These results also point to the potential importance of spatial extent in testing soil effects on plant poleward migration. Bertrand *et al.* (2012) did not find that soils impeded plant migration, possibly because their study was limited to the temperate forests of France, with fairly constrained soil heterogeneity, relative to that found from temperate forests to boreal forests and tundra. More SDM studies covering the latitudinal heterogeneity of soil properties across different continents and regions are required for a broader and deeper understanding of how soil conditions might influence distribution shifts under climate change.

Our results are in line with the relatively small number of manipulative experiments investigating the same question (e.g. Brown & Vellend, 2014; Collin *et al.*, 2016; Benning & Moeller, 2021a,b). For example, Brown and Vellend (2014) found that regeneration of sugar maple (*Acer saccharum*) from seed was lower in soil from beyond sugar maple's elevational range edge than in soil from within the range, when both were tested at low elevation in the field. Subsequent glasshouse experiments by Carteron *et al.* (2020) suggested that abiotic soil properties, particularly low cation exchange capacity, as well as a lack of endomycorrhizal fungi, were the main factors constraining seedling establishment of sugar maple in the soil of boreal forests. Benning and Moeller (2021a,b) found that the fitness of an

annual plant (*Clarkia xantiana*) was greater when grown in within-range soil than in beyond-range soil in the field. These studies with individual species, combined with our modelling results of many species, strongly suggest that soil conditions make important contributions to defining present and future range limits of plants.

Climate-only models predicting increased species richness in northern areas such as northern Québec (Bertheaux *et al.*, 2018) might overpredict the magnitude of such richness changes. Specifically, current soils in tundra and boreal forests, which are generally shallow, acidic and even frozen (permafrost) are likely to be unsuitable for many southern plant species (Lafleur *et al.*, 2010). Our results also indicate that the observed migration lags in some plant species under climate change (Fei *et al.*, 2017; Talluto *et al.*, 2017; Rumpf *et al.*, 2018; Boisvert-Marsh *et al.*, 2019; Rubenstein *et al.*, 2023) might be caused, at least partly, by unsuitable soil environments beyond leading range edges. While climate change and associated vegetation responses might alter some soil properties to make them more suitable for 'southern' species in the coming decades (e.g. the melting permafrost at tundra or reduced acidity following conifer-to-hardwood transitions), other soil properties, such as depth and texture, are likely to represent persistent barriers over much longer time frames. Plant colonization in higher latitudes may also require suitable microbial communities (Benning & Moeller, 2021b), such as mycorrhiza fungi, and the migration rates of these microbes can also influence the migration potential of plants, which are rarely studied yet. Whether plant species in the region possess the evolutionary potential to adapt to novel soil–climate combinations is an important open research question.

Although adding soil variables to SDMs frequently reduced the predicted area of suitable habitat (Fig. I in Notes S4), some areas, mainly around the Great Lakes, the Appalachian Mountains and the Southeastern USA, were actually predicted to have more species under future climate scenarios than in the climate-only model (Fig. 5). In the range shift analyses, we found that adding soil properties reduced shifts in northern range limits, without shifts in latitudinal ranges, which also suggests smaller shifts in southern range limits. Overall, edaphic conditions tend to decrease projected range shifts under climate change. One possible reason is that the suitable climate space was actually enlarged for some species after incorporating soil variables. While our results suggest generally less suitable soil conditions beyond current northern range limits in eastern North America, in principle the opposite could be true, such that once a climate constraint is lifted, migration is more likely in a climate + soil model than in a climate-only model (this might also help explain the results of Bertrand *et al.*, 2012). With correlated predictors, detecting and characterizing the effects of one variable (e.g. climate) can depend on inclusion of other correlated variables (e.g. soil; Bertrand *et al.*, 2012; Hájek *et al.*, 2022). In our study, it appears that SDM_{sc} was able to detect suitable climates in some southern areas in the future, which were not predicted to be suitable under the projections of $SDM_{climate}$. It is also possible that SDM_{sc} captured some soil environments that could act as refugia when climate change makes the relatively warm conditions in the south even

warmer. As such, $SDM_{climate}$ might overestimate extinction risk for populations at trailing range edges, for which SDM_{sc} can provide more useful assessments of habitat suitability for species' conservation (Hampe & Petit, 2005). SDMs have been widely applied in assessing plant extinction risk and plant conservation management (Corlett & Westcott, 2013; Zhang *et al.*, 2017; Song *et al.*, 2021), and our results highlight the necessity of incorporating soil properties not only to better understand the full range of constraints on distribution shifts but also the effects of climate itself. We might also expect interactive effects between climate and soil in determining plant distributions. For example, if there is a soil water availability threshold for species presence, then as rainfall declines, one would expect stronger effects of soil drainage on plant distributions (Jiang *et al.*, 2020). Interestingly, both SDM_{sc} and $SDM_{climate}$ projected increased suitable habitat areas under climate change (Fig. I in Notes S4), which may be a result of the geography of the region. In ENA, higher latitudes generally cover a wider range of longitudes than lower latitudes, such that a given climate space will cover a larger area as it shifts northwards. Here, we have only quantified species' suitable climate and soil conditions, recognizing that actual distribution shifts will also be influenced by dispersal limitation and biotic interactions (Guisan *et al.*, 2017).

Consistent with our third hypothesis, the importance of soil variables varied among species according to growth form and habitat type, albeit with most variation within groups. The extensive and deep root systems of trees should, on average, reduce their dependency on specific water or nutrient conditions (Schenk, 2008; Carmona *et al.*, 2021), which is consistent with the weaker soil effects we found for trees compared with herbs and shrubs (Fig. 2b). Beaugard and de Blois (2014) found similar results when comparing the importance of soil for the distributions of herbs vs trees. Lianas and vines (climbers) often have a ruderal growth strategy (Phillips *et al.*, 2002; Zhang *et al.*, 2021), which might promote persistence in variable soil habitats. With respect to habitat types, specific adaptations are required for growth in the water-logged and nutrient-poor environments of wetlands (Hájek *et al.*, 2022), likely explaining why wetland species showed somewhat stronger importance of soil variables than species from other habitats (Fig. 2c). Our study provides a preliminary exploration of this question, and multiple other factors, such as plant functional traits and range sizes (endemism), may also influence the relative importance of soil vs climate. Although we used relatively fine-scale soil data compared with previous studies, further tests of how and why soil constraints on distributions vary among species will likely require data at still finer scales.

Overall, it seems likely that our estimates of soil effects on plant distributions are conservative (or at least not overestimates), in that plants are likely to respond to soil variation at finer scales than the data we had available (250 m × 250 m). Although both climate and soil properties can vary at fine scales, soil properties are expected to show especially high spatial heterogeneity (Weil & Brady, 2013). For species of particular interest in conservation or management, accurately evaluating soil effects on distributions and predicting future habitats could fruitfully combine large-scale

analyses like the ones we have presented with targeted field studies with much finer-scale soil data in sites where the species is present or absent. We have revealed clear and important effects of soil properties on plant distributions and potential geographic range shifts, and we predict that future studies are likely to find even stronger effects by more closely matching occurrence and environmental data.

Acknowledgements

This study was supported by the Natural Sciences and Engineering Research Council of Canada, China Scholarship Council, and Compute Canada (<https://www.computecanada.ca/>). We thank Amael Le Squin, Huizhong Lu for the help of computation, and Brain Maitner, Brain Enquist, and other members of the BIEN working group for help in obtaining species occurrence data. We thank Tongli Wang for help with using the ClimateNA program. We thank Guillaume Blanchet, Dominique Gravel, Steven Kembel and members in Vellend Lab for comments and suggestions on this manuscript.

Competing interests

None declared.

Author contributions

MN and MV conceived the project and wrote the manuscript. MN collected the data and performed the analyses.

ORCID

Ming Ni  <https://orcid.org/0000-0002-5180-1049>

Mark Vellend  <https://orcid.org/0000-0002-2491-956X>

Data availability

The species occurrence data are available at <https://bien.nceas.ucsb.edu/bien/biendata/bien-4/>. The projected species maps are available on request from the corresponding author (*c.* 5 TB in total, too large for public repositories). The predictor importance and the projected range shifts of species' suitable habitats are provided in the supporting information (Notes S6).

References

- Araújo MB, New M. 2007. Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* 22: 42–47.
- Bahram M, Hildebrand F, Forslund SK, Anderson JL, Soudzilovskaia NA, Bodegom PM, Bengtsson-Palme J, Anslan S, Coelho LP, Harend H *et al.* 2018. Structure and function of the global topsoil microbiome. *Nature* 560: 233–237.
- Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* 3: 327–338.
- Beauregard F, de Blois S. 2014. Beyond a climate-centric view of plant distribution: edaphic variables add value to distribution models. *PLoS ONE* 9: e92642.
- Benning JW, Moeller DA. 2021a. Microbes, mutualism, and range margins: testing the fitness consequences of soil microbial communities across and beyond a native plant's range. *New Phytologist* 229: 2886–2900.
- Benning JW, Moeller DA. 2021b. Plant–soil interactions limit lifetime fitness outside a native plant's geographic range margin. *Ecology* 102: e03254.
- Berteaux D, Ricard M, St-Laurent MH, Casajus N, Périé C, Beauregard F, de Blois S. 2018. Northern protected areas will become important refuges for biodiversity tracking suitable climates. *Scientific Reports* 8: 1–9.
- Bertrand R, Perez V, Gégout J. 2012. Disregarding the edaphic dimension in species distribution models leads to the omission of crucial spatial information under climate change: the case of *Quercus pubescens* in France. *Global Change Biology* 18: 2648–2660.
- Blomberg SP, Garland T Jr, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57: 717–745.
- Boisvert-Marsh L, Périé C, de Blois S. 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. *Journal of Ecology* 107: 1956–1969.
- Brown C, Vellend M. 2014. Non-climatic constraints on upper elevational plant range expansion under climate change. *Proceedings of the Royal Society B: Biological Sciences* 281: 20141779.
- Carmona CP, Bueno CG, Toussaint A, Träger S, Díaz S, Moora M, Munson AD, Pärtel M, Zobel M, Tamme R. 2021. Fine-root traits in the global spectrum of plant form and function. *Nature* 597: 683–687.
- Carteron A, Parasquive V, Blanchard F, Guilbeault-Mayers X, Turner BL, Vellend M, Laliberté E. 2020. Soil abiotic and biotic properties constrain the establishment of a dominant temperate tree into boreal forests. *Journal of Ecology* 108: 931–944.
- Chauvier Y, Thuiller W, Brun P, Lavergne S, Descombes P, Karger DN, Renaud J, Zimmermann NE. 2021. Influence of climate, soil, and land cover on plant species distribution in the European Alps. *Ecological Monographs* 91: e01433.
- Collin A, Messier C, Bélanger N. 2016. Conifer presence may negatively affect sugar maple's ability to migrate into the boreal forest through reduced foliar nutritional status. *Ecosystems* 20: 701–716.
- Corlett RT, Westcott DA. 2013. Will plant movements keep up with climate change? *Trends in Ecology and Evolution* 28: 482–488.
- Donaldson JE, Hui C, Richardson DM, Robertson MP, Webber BL, Wilson JR. 2014. Invasion trajectory of alien trees: the role of introduction pathway and planting history. *Global Change Biology* 20: 1527–1537.
- Dyderski MK, Paž S, Frelich LE, Jagodziński AM. 2018. How much does climate change threaten European forest tree species distributions? *Global Change Biology* 24: 1150–1163.
- Enquist BJ, Condit R, Peet RK, Schildhauer M, Thiers BM. 2016. Cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity. *PeerJ Preprints* 4: e2615v2.
- Fei S, Desprez JM, Potter KM, Jo I, Knott JA, Oswalt CM. 2017. Divergence of species responses to climate change. *Science Advances* 3: e1603055.
- Flora of North America Editorial Committee, ed. 1993. Flora of North America North of Mexico [Online], vols. 22. New York, NY, USA and Oxford, UK. [WWW document] URL <http://beta.floranorthamerica.org> [accessed 15 September 2021].
- Ford KR, HilleRisLambers J. 2020. Soil alters seedling establishment responses to climate. *Ecology Letters* 23: 140–148.
- Fricke EC, Ordóñez A, Rogers HS, Svenning JC. 2022. The effects of defaunation on plants' capacity to track climate change. *Science* 375: 210–214.
- Gleason HA, Cronquist A. 1991. *Manual of vascular plants of northeastern United States and adjacent Canada*, 2nd edn. Princeton, NJ, USA: van Nostrand.
- Greiser C, Hylander K, Meineri E, Luoto M, Ehrlén J. 2020. Climate limitation at the cold edge: contrasting perspectives from species distribution modelling and a transplant experiment. *Ecography* 43: 637–647.
- Guisan A, Thuiller W, Zimmermann NE. 2017. *Habitat suitability and distribution models*. Cambridge, UK: Cambridge University Press.
- Hájek M, Těšitel J, Tahvanainen T, Peterka T, Jiménez-Alfaro B, Jansen F, Pérez-Haase A, Garbolino E, Carbognani M, Kolari THM *et al.* 2022. Rising temperature modulates pH niches of fen species. *Global Change Biology* 28: 1023–1037.

- Hampe A, Petit RJ. 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* 8: 461–467.
- Hengl T. 2018. Global DEM derivatives at 250 m, 1 km and 2 km based on the MERIT DEM (1.0). *Zenodo*. doi: 10.5281/zenodo.1447210.
- Hengl T, de Jesus JM, Heuvelink GBM, Gonzalez MR, Kilibarda M, Blagotić A, Shangguan W, Wright MN, Geng X, Bauer-Marschallinger B *et al.* 2017. SoilGrids250m: global gridded soil information based on machine learning. *PLoS ONE* 12: e0169748.
- Iverson LR, Prasad AM, Matthews SN, Peters M. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management* 254: 390–406.
- Jiang Z, Liu H, Wang H, Peng J, Meersmans J, Green SM, Quine TA, Wu X, Song Z. 2020. Bedrock geochemistry influences vegetation growth by regulating the regolith water holding capacity. *Nature Communications* 11: 2392.
- Jin Y, Qian H. 2019. V.PHYLOMAKER: an R package that can generate very large phylogenies for vascular plants. *Ecography* 42: 1353–1359.
- Lafleur B, Paré D, Munson AD, Bergeron Y. 2010. Response of northeastern North American forests to climate change: will soil conditions constrain tree species migration? *Environmental Reviews* 18: 279–289.
- Larcher W. 2003. *Physiological plant ecology, ecophysiology and stress physiology of functional groups*. New York, NY, USA: Springer.
- Lenoir J, Svenning JC. 2014. Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography* 38: 15–28.
- Luo W, Ni M, Wang Y, Lan R, Eissenstat DM, Cahill JF, Li B, Chu C. 2021. Limited evidence of vertical fine-root segregation in a subtropical forest. *New Phytologist* 231: 2308–2318.
- Maitner BS, Boyle B, Casler N, Condit R, Donoghue J, Durán SM, Guaderrama D, Hinchliff CE, Jørgensen PM, Kraft NJB *et al.* 2018. The BIEN R package: a tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution* 9: 373–379.
- Michaelis J, Pannek A, Diekmann M. 2016. Soil pH limits of forest vascular plants determine range size and threat level. *Journal of Vegetation Science* 27: 535–544.
- Morin X, Lechowicz MJ. 2012. Niche breadth and range area in North American trees. *Ecography* 36: 300–312.
- Naimi B, Araújo MB. 2016. sdm: a reproducible and extensible R platform for species distribution modelling. *Ecography* 39: 368–375.
- Ni M, Vellend M. 2021. Space-for-time inferences about range-edge dynamics of tree species can be influenced by sampling biases. *Global Change Biology* 27: 2102–2112.
- Phillips OL, Martínez RV, Arroyo L, Baker TR, Killeen T, Lewis SL, Malhi Y, Mendoza AM, Neill D, Vargas PN *et al.* 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418: 770–774.
- R Core Team. 2020. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Rubenstein MA, Weiskopf SR, Bertrand R, Carter SL, Comte L, Eaton MJ, Johnson CG, Lenoir J, Lynch AJ, Miller BW *et al.* 2023. Climate change and the global redistribution of biodiversity: substantial variation in empirical support for expected range shifts. *Environmental Evidence* 12: 1–21.
- Rumpf SB, Hülber K, Klöner G, Moser D, Schütz M, Wessely J, Willner W, Zimmermann NE, Dullinger S. 2018. Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences, USA* 115: 1848–1853.
- Schenk HJ. 2008. Soil depth, plant rooting strategies and species' niches. *New Phytologist* 178: 223–225.
- Schenk HJ, Jackson RB. 2002. The global biogeography of roots. *Ecological Monographs* 72: 311–328.
- Siefert A, Ravenscroft C, Althoff D, Alvarez-Yépiz JC, Carter BE, Glennon KL, Heberling JM, Jo IS, Pontes A, Sauer A *et al.* 2012. Scale dependence of vegetation–environment relationships: a meta-analysis of multivariate data. *Journal of Vegetation Science* 23: 942–951.
- Song H, Ordonez A, Svenning J, Qian H, Yin X, Mao L, Deng T, Zhang J. 2021. Regional disparity in extinction risk: comparison of disjunct plant genera between eastern Asia and eastern North America. *Global Change Biology* 27: 1904–1914.
- Talluto MV, Boulangeat I, Vissault S, Thuiller W, Gravel D. 2017. Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nature Ecology & Evolution* 1: 182.
- Thuiller W. 2007. Biodiversity: climate change and the ecologist. *Nature* 448: 550–552.
- Thuiller W, Lavergne S, Roquet C, Boulangeat I, Lafourcade B, Araujo M, B. 2011. Consequences of climate change on the tree of life in Europe. *Nature* 470: 531–534.
- USDA, NRCS. 2023. The PLANTS database. Greensboro, NC, USA: National Plant Data Team. [WWW document] URL <http://plants.usda.gov> [accessed 24 July 2023].
- Walther L, Meier ES. 2017. Tree species distribution in temperate forests is more influenced by soil than by climate. *Ecology and Evolution* 7: 9473–9484.
- Wang T, Hamann A, Spittlehouse D, Carroll C. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE* 11: e0156720.
- Weil R, Brady NC. 2013. *Nature and properties of soils*. The Pearson New International Edition. Boston, MA, USA: Pearson Higher Ed.
- Woldemeskel FM, Sharma A, Sivakumar B, Mehrotra R. 2012. An error estimation method for precipitation and temperature projections for future climates. *Journal of Geophysical Research: Atmospheres* 117: D22104.
- Zhang J, Nielsen SE, Chen Y, Georges D, Qin Y, Wang S, Svenning J, Thuiller W. 2017. Extinction risk of North American seed plants elevated by climate and land-use change. *Journal of Applied Ecology* 54: 303–312.
- Zhang K-Y, Yang D, Zhang Y-B, Ellsworth DS, Xu K, Zhang Y-P, Chen Y-J, He F, Zhang J-L. 2021. Differentiation in stem and leaf traits among sympatric lianas, scandent shrubs and trees in a subalpine cold temperate forest. *Tree Physiology* 41: tpab049.
- Zimmermann NE, Edwards TC Jr, Moisen GG, Frescino TS, Blackard JA. 2007. Remote sensing-based predictors improve distribution models of rare, early successional and broadleaf tree species in Utah. *Journal of Applied Ecology* 44: 1057–1067.

Supporting Information

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

Notes S1 Full list of environmental variables and Pearson's correlations.

Notes S2 Tests for phylogenetic signal in the soil/climate importance across species.

Notes S3 Differences in the relative importance of climate variables across species.

Notes S4 Comparison of model performance and predictions between SDM_{sc} and $SDM_{climate}$.

Notes S5 Model results for endemic plants in eastern North America.

Notes S6 Data on variable importance and projected range shifts.

Please note: Wiley is not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.