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Research article

A tree's view of the terrain: downscaling bioclimate variables to high resolution using a novel multi-level species distribution model

Matthew M. Kling[1,2], **Kathryn C. Baer**[3] and **David D. Ackerly**[1,4]

[1]Department of Integrative Biology, University of California, Berkeley, CA, USA
[2]Department of Biology and Gund Institute for the Environment, University of Vermont, Burlington, VT, USA
[3]USDA Forest Service, Pacific Northwest Research Station Anchorage Forestry Sciences Laboratory, Anchorage, AK, USA
[4]Department of Environmental Science, Policy and Management, University of California, Berkeley, CA, USA

Correspondence: Matthew M. Kling (mattkling@berkeley.edu)

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Fine-scale spatial climate variation fosters biodiversity and buffers it from climate change, but ecological studies are constrained by the limited accessibility of relevant fine-scale climate data. In this paper we introduce a novel form of species distribution model that uses species occurrences to predict high-resolution climate variation. This new category of 'bioclimate' data, representing micro-scale climate as experienced by one or more species of interest, is a useful complement to microclimate data from existing approaches. The modeling method, called BISHOP for 'bioclimate inference from species' high-resolution occurrence patterns,' uses data on species occurrences, coarse-scale climate, and fine-scale physiography (e.g. terrain, soil, vegetation) to triangulate fine-scale bioclimate patterns. It works by pairing a climate-downscaling function predicting a latent bioclimate variable, with a niche function predicting species occurrences from bioclimate. BISHOP infers how physiography affects bioclimate, estimates how these effects vary geographically, and produces high-resolution (10 m) maps of bioclimate over large regions. It also predicts species distributions. After introducing this approach, we apply it in an empirical study focused on topography and trees. Using data on 216 North American tree species, we document the biogeographic patterns that enable BISHOP, estimate how four terrain variables (northness, eastness, windward exposure, and elevational position) each influence three climate variables, and use these results to produce downscaled maps of tree-specific bioclimate. Model validation demonstrates that inferred bioclimate outperforms macroclimate in predicting distributions of separate species not used during inference, confirming its ecological relevance. Our results show that nearby bioclimates can differ by 5°C in temperature and twofold in moisture, with equator-facing, east-facing, windward-facing, and locally elevated sites exhibiting hotter, drier bioclimates on average. But these effects vary greatly across climate zones, revealing that topographically similar landscapes can differ strongly in their bioclimate variation. These results have important implications for micrometeorology, biodiversity, and climate resilience.

Keywords: ecological modeling, forest ecology, microclimate, species distributions, topography

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Introduction

Background: a climate data shortfall

Ecological patterns like species occurrences, population demographic rates, and vegetation gradients arise from organisms' experiences of environmental variation at extremely fine spatial scales, integrated over long temporal scales spanning the lifetimes of individuals and populations in a given location. Understanding the climate variation that drives these emergent phenomena is essential for basic ecology, and also for conservation, since climate heterogeneity helps to foster high biodiversity and buffer it from climate change (Dobrowski 2011, Scherrer and Körner 2011, McLaughlin et al. 2017, Suggitt et al. 2018, De Frenne et al. 2019). Yet we lack a category of spatial climate data that would be optimal for studying these biogeographic phenomena: data with high spatial resolution, low temporal resolution, and inherent ecological relevance to the species being studied.

Macroclimate data are the most readily available and widely used form of spatial climate data, and have a temporal scale ranging from years to decades that is well suited to studying time-integrated ecological patterns. But with a spatial resolution generally no finer than 1 km, these data capture only the climatic effects of coarse features like latitude, elevation, and continentality. They neglect microclimate patterns that arise from fine-scale physiographic features including terrain, vegetation, and soils that generate climate variation among nearby microsites (Geiger et al. 2009, Zellweger et al. 2020), an omission that has led to limitations and biases in global change research (Franklin et al. 2013, Potter et al. 2013, Nadeau et al. 2017).

Microclimate data do account for these fine-scale patterns and are becoming increasingly accessible (Bramer et al. 2018, Maclean et al. 2019, Lembrechts et al. 2020), but they have limitations. Mechanistic microclimate models that directly represent fine-scale meteorological physics have many advantages, but their accuracy depends on large volumes of high-resolution input data (e.g., leaf angle and leaf area index) that is often unavailable over large regions. Empirical models that correlate fine-scale variables like terrain and vegetation with measurements from in situ microclimate sensors offer a good solution (Bramer et al. 2018, John et al. 2024), but require that researchers either install their own sensors throughout a landscape of interest, or utilize global microclimate databases like SoilTemp (Lembrechts et al. 2020) that have geographic biases and may not be openly accessible.

Additionally, even with microclimate data in hand, barriers arise in incorporating them into many kinds of spatial ecological studies. Microclimate models typically produce high temporal frequency estimates of extremely specific meteorological variables (e.g. hourly time series of temperature 5 cm above the soil surface in a closed-canopy forest on particular dates (Maclean et al. 2019)), sometimes for numerous vertical strata across a site. Choosing among and summarizing these variables to match the temporal scale of ecological studies can be complex in both theory and practice. And while they may provide objective measures of certain aspects of the environment, a given variable may have limited relevance to the ecology of an individual species, especially considering the integrated impacts of environment on all aspects of the life history which determine whether a species is able to persist at a particular site.

Many of these issues can be addressed by using species occurrences themselves as climate indicators. Species occurrence data are widely available, are often highly localized (particularly for sessile organisms like plants), and integrate over ecological and physical uncertainties to capture the salient patterns of long-term climate variation as experienced by a species. There is a long history in ecology of using plants as climate indicators, including inferring climate from fossils ('paleoclimate proxies' (Lyell 1837, Mauri et al. 2015)), from the performance of individuals transplanted into a site ('phytometers' (Clements and Goldsmith 1924, Strobl et al. 2018)), and from the observed species composition of the naturally occurring plant community ('indicator species' (Ellenberg et al. 1992, Diekmann 2003)). More recently, methods including latent-variable species distribution models (SDMs) (McInerny and Purves 2011, Keil et al. 2013), climate indicator interpolation models (Karlsen et al. 2005, Scherrer and Körner 2011), and microclimate heterogeneity estimators (Lenoir et al. 2013) have continued to expand the statistical tools available for using species occurrences to model fine-scale climate variation. But we are not aware of an existing approach that can use occurrences to predict and map high-resolution climate patterns, in native units like degrees Celsius, beyond the plots where species were recorded.

Novel method: refactoring an SDM to downscale climate variables

In this paper we introduce a new form of SDM that leverages species occurrence data, in combination with data on macroclimate and fine-scale physiography, to predict patterns of high-resolution climate as experienced by the focal species (Fig. 1). We call this biologically inferred fine-scale climate variation 'bioclimate', and we call the modeling method 'bioclimate inference from species' high-resolution occurrence patterns' (BISHOP). The approach integrates components from a range of other methods, including indicator species models, latent-variable species distribution models, and empirical microclimate models.

A traditional SDM structure would either ignore microphysiography or assume that it, along with macroclimate, directly predicts species occurrence probability. A BISHOP model instead assumes that macroclimate and micro-physiography shape an unmeasured bioclimate variable that then drives occurrence probability. The climate downscaling submodel predicts a higher-resolution version of a macroclimate variable, creating its corresponding bioclimate variable by adding an offset (or Δ value) that is a function of fine-scale physiography (e.g. terrain, soils, vegetation). If one had field-based microclimate measurements, then the coefficients on these physiographic variables could be inferred as in a typical empirical microclimate model. Instead, these values are inferred from the occurrence patterns of one or more indicator species as is done in latent-variable SDMs (McInerny

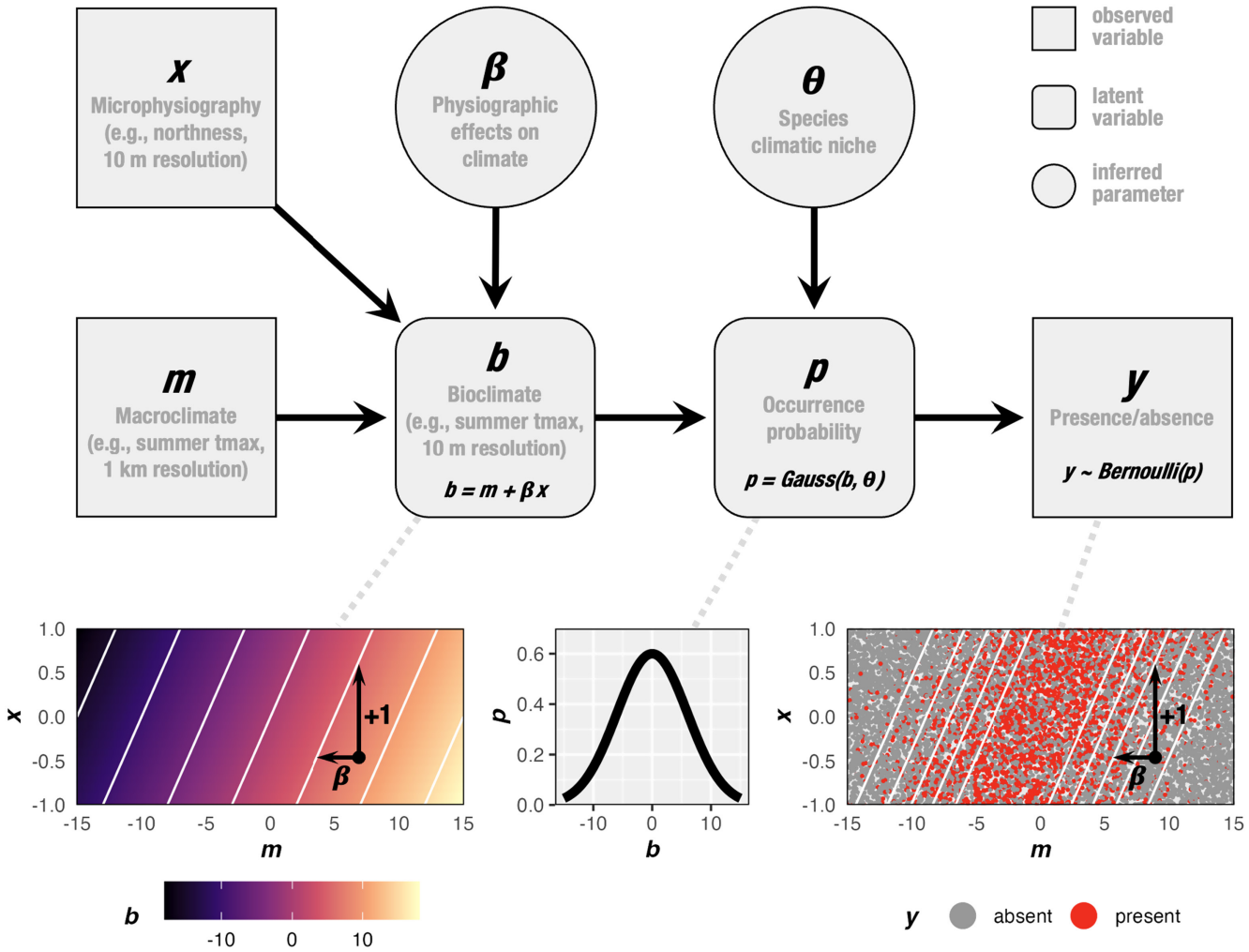

Figure 1. Structure of a bioclimate inference from species' high-resolution occurrence patterns (BISHOP) model, a form of species distribution model (SDM) factored to infer and project high-resolution bioclimate in addition to species occurrence probability. The approach works by separating the typical SDM response function into two components: a bioclimate equation representing how fine-scale physiography (x, e.g. terrain, soil, or vegetation structure) modifies coarse-scale macroclimate (m, e.g. temperature or precipitation) to determine 'bioclimate' (b, fine-scale climate as experienced by the species), and a niche equation representing how bioclimate predicts species occurrence probability (p). Arrows in the structural diagram indicate presumed causation. In the bottom row, the righthand plot shows an example relationship among the three input variables, with presences (red points) following a commonly observed parallelogram shape in which species are increasingly restricted to north-facing slopes in macroclimatically warmer parts of their range (Ackerly et al. 2020). From this pattern, the model can jointly infer the species niche parameters (θ, describing the shape of a Gaussian bell curve illustrated at center) and the physiographic parameters (β, illustrated at left). This example uses a value of $\beta = -3$, which determines the angle of the isoclines shown in white on the lower plots. Note that while this figure illustrates a minimal version of the model, components can be added to accommodate multiple physiographic and climatic variables, multiple indicator species, and/or geographic variation in physiographic effects.

and Purves 2011). The traditional SDM and BISHOP model both predict species occurrences from the same input variables, but in BISHOP's case predicting distributions is only an incidental side effect. BISHOP's primary, differentiating features are that it also predicts bioclimate, infers meaningful parameters quantifying how physiography shapes bioclimate, and infers a physiographically controlled version of species climatic niches. It is thus useful as a tool for a range of applications separate from the traditional SDM.

This approach works by quantifying well-known relationships among macroclimate, fine-scale physiography, and species occurrences. Consider, for example, the general pattern (shown in the scatter plot in Fig. 1) that across its geographic range, a plant species tends to be restricted to shadier pole-facing hillslopes in warm landscapes, to occupy a wide range of hillslopes in intermediate-temperature landscapes, and to be restricted to sunnier equator-facing hillslopes in landscapes near its cold range limit (Boyko 1947, Ackerly et al. 2020). These patterns presumably arise as a result of unmeasured fine-scale climate variation mediating the relationships between macroclimate, topography, and species occurrences. In this example, one could quantify the

rate at which a species shifts onto increasingly pole-facing slopes as macroclimate warms (diagonal contours in Fig. 1), which provides an estimate of how northness influences temperature from the perspective of the focal species. An effect size like this can be studied directly for its biological or meteorological interest, or used to generate downscaled bioclimate maps for other ecological applications.

Bioclimate inferred from species distributions could be a valuable complement to traditional microclimate estimates, helping fill the gap between existing macroclimate and microclimate data that limits research in biodiversity and conservation. These bioclimate variables are downscaled versions of the input macroclimate variables and carry the same units, but they are not directly comparable to traditional microclimate estimates, and the two should not be expected to precisely match. Instead, the bioclimate variables provide an inference or estimate of how the particular species of interest experiences fine-scale spatial climate variation integrated over long timeframes. Because not every species experiences microclimate in the same way, bioclimate variables will not necessarily be transferable among taxa.

While the above examples illustrate the simplest version of a BISHOP model, the model can be further extended. For example, the empirical analysis in this paper extends this model to a multivariate climate context, adds an additional model level representing how physiography–bioclimate parameters vary spatially as a function of other variables, and adds a hierarchical SDM module that allows multiple species to jointly inform the bioclimatic inferences (Supporting information). Although our analysis uses an unusually large multispecies dataset, this is not a prerequisite for the BISHOP approach, which, like a traditional SDM, can be used on smaller datasets that are more readily available.

Empirical application: topography and trees

This modeling approach could be applied in a range of systems. Here, we use it to quantify how fine-scale terrain influences bioclimate from the perspective of tree species distributions across North America. Fine-scale presence–absence patterns of mature trees serve as an integrated indicator of all the microclimate conditions that influence a species' growth and survival, including the effects of underground, near-ground, and canopy-level microclimates on seedling, sapling, and adult trees.

We focus on three climate variables important to trees: summer daytime maximum temperature, winter nighttime minimum temperature, and annual precipitation (which for brevity we call 'high temperature,' 'low temperature,' and 'moisture', respectively). Our analysis is based on 216 tree species across hundreds of thousands of plots surveyed for the USDA Forest Service Forest Inventory and Analysis Program (FIA) (Bechtold and Patterson 2005) and Canada's National Forest Inventory (NFI) (Gillis et al. 2005). While the simultaneous use of many indicator species helps to refine bioclimate estimates and identify macroecological patterns, we also demonstrate use of the BISHOP approach with data for individual species.

Fine-scale terrain is a primary driver of microclimate variation in many regions (Geiger et al. 2009, Dobrowski 2011). (Vegetation also plays a key microclimate role (De Frenne et al. 2019), and forest structure variables could easily be incorporated alongside terrain in this modeling framework, but since our study uses trees as indicator species we avoid vegetation predictors as they would introduce circularity.) We quantify how four terrain variables – northness, eastness, windward exposure, and elevational position relative to the surrounding landscape (Fig. 2) – each influence the three climate variables mentioned above, for a total of 12 'topoclimate effects'. These four micro-topographic axes influence a site's exposure to sun and wind as well as flows of air and water across the terrain, which in turn govern the temperature and moisture of its microclimate (Fig. 2). The physical mechanisms connecting these terrain variables to microclimate are complex, involving interactions and feedbacks at multiple scales (Holland and Steyn 1975, Dai et al. 1999, Geiger et al. 2009, Moeslund et al. 2013, Davis et al. 2019, Pastore et al. 2024). These direct effects also influence mediating variables like vegetation and soil that then themselves shape microclimate (Boerner 2006, Moeslund et al. 2013, Davis et al. 2019, De Frenne et al. 2019) (Fig. 3).

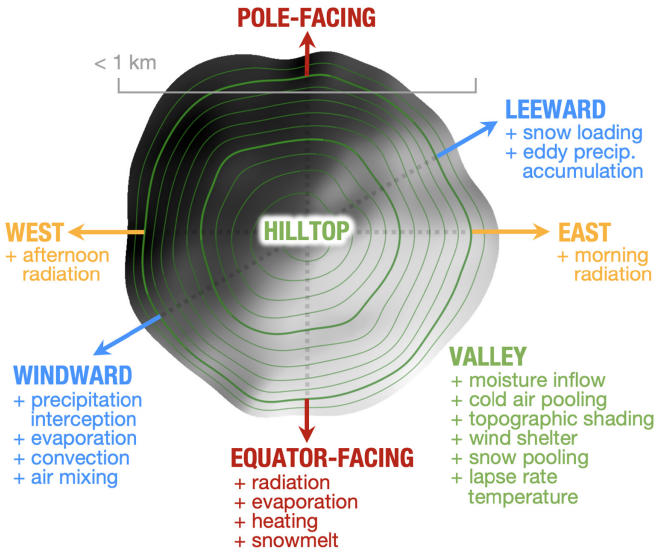

Figure 2. Processes through which fine-scale terrain shapes microclimate. Looking down on a hypothetical hill, arrows and contours illustrate the four topographic axes in our analysis, with micrometeorological rates listed at the end of the axes where they are expected to be higher. The north–south dimension is quantified as 'northness', which measures how steeply a site faces the north. The east–west axis, 'eastness', measures how steeply a site faces the east. 'Windward exposure' indicates how steeply a site faces into the prevailing wind; the orientation of this axis varies but is pictured here as coming from the southwest since that is typical in our study area. Elevational position, the valley–hilltop axis sometimes called 'topographic position index', is indicated by the contour lines and has low values at the bottom of all sides of this hill (the text placement is arbitrary). All four variables would have values of zero for a site in a uniformly level landscape.

Importantly, these topoclimate effects are expected to vary geographically due to factors like sun angle, cloud cover, moisture availability, and wind regimes (Holland and Steyn 1975, Dai et al. 1999, Geiger et al. 2009, Moeslund et al. 2013, Davis et al. 2019), and understanding this variation is a goal in ecology and micrometeorology. In our analysis we infer how each of the 12 topoclimate effects varies across climate zones as a function of two 'modifier' variables: macroclimate temperature and precipitation. Temperature is an important predictor because phenomena like snow albedo feedbacks, latent heat flux, blackbody radiation rates, and sun angle differences (by correlation with latitude) vary across temperature gradients (Campbell and Norman 2000, Geiger et al. 2009). Precipitation is expected to influence topoclimate effects because moisture alters the balance between sensible and latent heat fluxes and the balance among windward effects, and because associated cloud cover scatters incoming sunlight and reflects outgoing longwave radiation (Campbell and Norman 2000, Geiger et al. 2009). Other important effect-modifying variables like latitude and cloud cover were not included directly because of their high correlations with temperature and precipitation, but they likely explain some of the inferred temperature and precipitation effects due to these correlations.

Our analysis has four empirical goals. First, we illustrate basic relationships between a landscape's macroclimate and

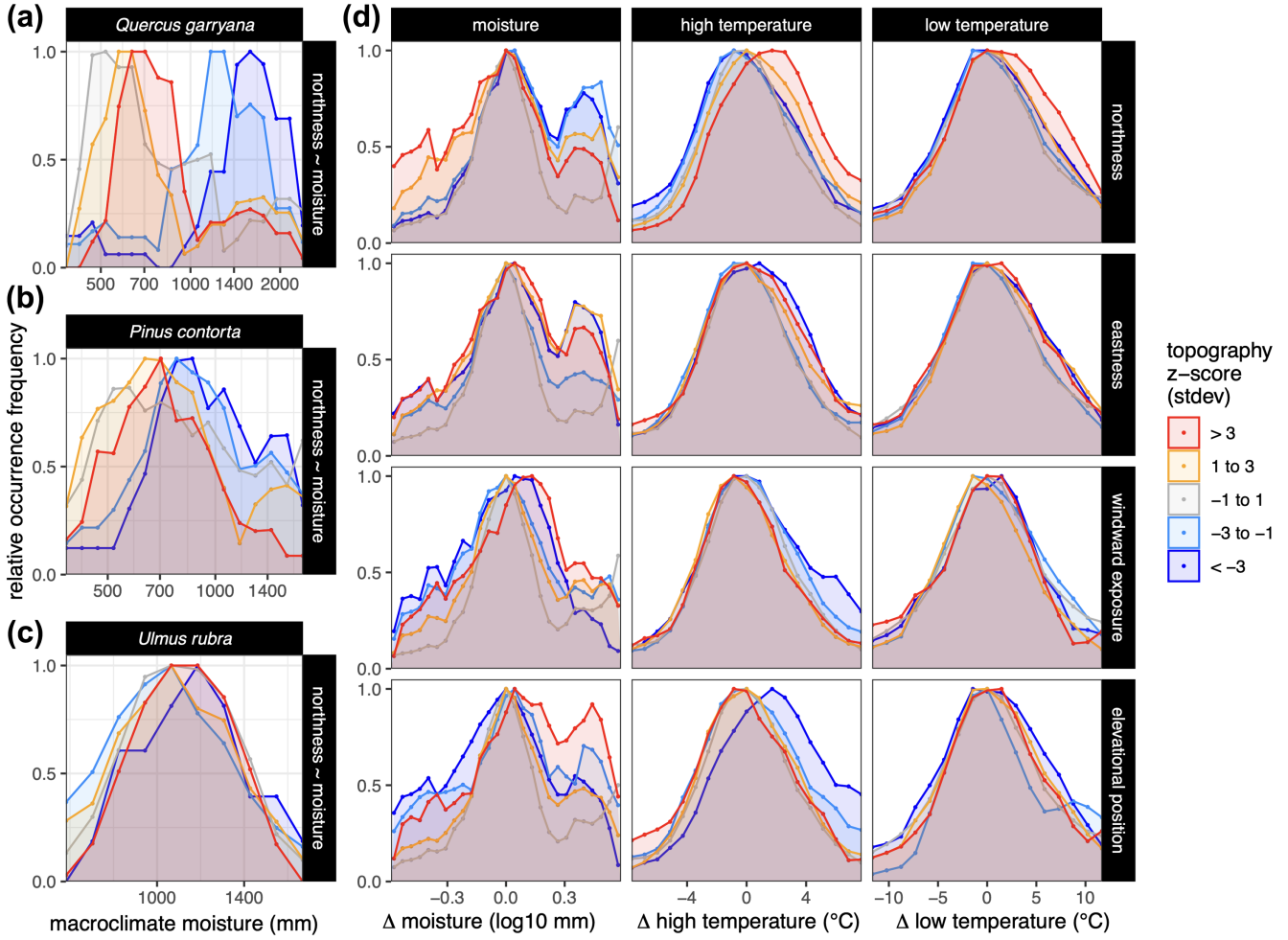

Figure 3. Species occurrence probability as a function of topography and macroclimate, summarized from forest inventory data without modeling. (a–c) Relationships between macroclimate moisture (x-axis) and northness (color) across the ranges of three example species; for a given combination of macroclimate and topographic values, y-values represent the relative proportion of forest inventory plots occupied by the species. These are specific cases of the general pattern shown in the upper-left panel of (d). (d) Mean relationships across all 216 species in the analysis, for each combination of topographic variable (listed at right) and climate variable (listed at top); the macroclimate values on the x-axis represent the plot macroclimate minus the average macroclimate across plots occupied by a species. As an example to demonstrate interpretation, consider the bottom-center panel of (d), which shows relationships between macroclimate summer high temperature (x-axis) and plot elevational position (color): the horizontal offset between the dark red curve (highly prominent sites) and dark blue curve (highly depressed sites) indicates that the difference between these topographic positions corresponds to roughly 3°C on average, while the vertical differences indicate that for example in a landscape 6°C hotter than its average, the typical species is roughly three times more likely to occur in a highly depressed plot as a highly prominent plot. Topographic variables are standardized for comparability.

the fine-scale topographic distributions of tree species within the landscape. Second, we use a BISHOP model to infer how the topographic variables affect each climate variable, and how these effects vary across climate zones. Third, we evaluate how these inferred bioclimates compare to macroclimate as predictors of tree species distributions. Last, we show how these results can be used to generate downscaled (10 m) maps of bioclimate as experienced by trees.

Material and methods

Species occurrences

Our analysis is based on forest inventory data from FIA (Bechtold and Patterson 2005) and NFI (Gillis et al. 2005). Seedling occurrences were not used since they may not reflect conditions suitable for long-term species persistence. From FIA we used the 'tree' dataset; in addition to the main FIA dataset covering the continental USA and coastal Alaska, we used FIA data from parts of interior Alaska. From NFI we used the ground plot 'large trees' dataset. We excluded plots with stocking or harvesting, reconciled FIA–NFI taxonomy differences, and removed species with fewer than 100 occurrences. FIA plots each have four subplots, while NFI does not have subplots; we did all analyses at the FIA subplot and NFI plot level, and for simplicity refer to these as 'plots' hereafter. For plots surveyed multiple times, we considered a species present if it was recorded in any survey. We used confidential exact FIA and NFI plot locations.

Topoclimate variables

We compiled several variables for each plot, including tree species occurrences, four topographic variables (northness, eastness, windward exposure, and elevational position (Theobald et al. 2015, USGS 2019, Kling and Ackerly 2020)), three primary macroclimate variables (total annual precipitation, maximum temperature of the warmest month, and minimum temperature of the coldest month (Karger et al. 2017)), and two effect modifiers (mean annual temperature and total annual precipitation). Whereas the 'macroclimate variables' get modified by topography to become bioclimate variables and in turn shape species distributions, the 'effect modifiers' are simply predictors that are hypothesized to influence the strength of those topoclimate effects; the modifiers we chose happen also to be climate variables, for the reasons described above. See the Supporting information for details.

Data distillation

Prior to modeling, we standardized all topographic and macroclimate variables. For each species, we generated a distinct occurrence dataset representing presences and absences across climatic and topographic gradients, and then summarized these continuous data into a set of discrete multivariate bins to reduce the dataset size for computational reasons. Data for all species were then combined into a single table. See the Supporting information for details.

Species' topoclimate distributions

To examine the relationships between a landscape's macroclimate and the topographic positions species occupy within the landscape, we grouped plots into bivariate macroclimate-by-topography bins and visualized the relative occurrence frequencies for each species in each bin. While these summaries are useful for illustrating topoclimate effects, a statistical model is needed to control for confounders such as spatial covariance or multivariate niche shapes.

Statistical bioclimate model

We used the distilled data to fit a multilevel Bayesian model describing species occurrence probabilities as a function of macroclimate and topography. The model includes a climate downscaling component that models a latent bioclimate variable as a function of macroclimate and topography, and a niche component that models species occurrences as a function of bioclimate (Fig. 1, Supporting information). By jointly inferring both sets of parameters, we can estimate the niche shapes and topoclimate effects that together best fit observed species occurrence patterns.

The model makes the following basic assumptions: 1) the difference between a site's macroclimate and its bioclimate is a function of topography. 2) Each macroclimate variable has a corresponding bioclimate variable, and these are equal in a flat site. 3) At a given site, each topographic variable has a linear modifying effect on each macroclimate variable. 4) These effects vary among locations as a spline function of the modifier variables. 5) The probability of a species occurring on a plot is a multivariate bell-shaped niche function of the plot's bioclimate. 6) Any additional variables omitted from the model are not correlated with the included variables in ways that would bias inference.

While none of these assumptions perfectly reflects the real world, they represent reasonable approximations that make the model tractable. For example, the second assumption that bioclimate and macroclimate are equal on a flat site is imperfect – microclimate is not simply fine-scale macroclimate – but adding an additional intercept term to account for the difference would make the model unidentifiable because the parameters for the intercept and the species niche optimum would be colinear.

We fit two versions of the model. In the 'full' multi-species model that is the primary focus of our empirical results, data from all 216 species were jointly used to quantify bioclimate effects for North American trees and to infer how these effects vary as a function of modifier variables. In a second 'minimal' version of the model that is simpler to implement in other studies, data from one species at a time were used to estimate average topography–microclimate effects across the species' range.

We evaluated model performance by examining MCMC diagnostics, by using simulated data to test parameter estimation, and by evaluating the model's ability to reproduce

the 'species topoclimate distributions' mentioned above. In addition, while BISHOP was conceived to study bioclimate rather than to predict species distributions, understanding its performance in predicting distributions is still informative. As a way to test the ecological relevance of BISHOP-inferred bioclimate variables, we compared the performance of bioclimate versus macroclimate as predictors of species occurrences. And as context for its utility as an SDM, we compared BISHOP to a standard SDM that was fit with the same macroclimate and topographic predictors but without the latent bioclimate component. Both these evaluations measured performance using cross-validation on withheld testing data. See the Supporting information for details on model structure, fitting and evaluation.

Climate downscaling

We used the fitted multi-species model to generate downscaled tree-species bioclimate data for an example 6 × 13 km landscape in southern Idaho, USA (−112°39′E, 42°34′N). The inputs were the same macroclimate and wind data used to fit the model, and a 10 m elevation raster (USGS 2019). We used bilinear interpolation to create smoothed macroclimate variables at 10 m resolution, and used elevation to calculate the four topographic variables at 10 m resolution. Using the fitted model parameters, we then calculated bioclimate high temperature, low temperature, and moisture on the 10 m grid. This process is illustrated in the Supporting information.

This process can be easily replicated using an R package (see Data availability section) that lets users input elevation data for any landscape in our study area to generate bioclimate estimates for North American trees based on coefficients from the multi-species model. To yield consistent results, elevation data should have a resolution similar to our input data (10–100 m), and cover an area of multiple square kilometers. The model can provide reasonable estimates only within the continental USA and Canada, so the tool does not allow extrapolation beyond this region.

All analysis was done in R (www.r-project.org) and Stan (Carpenter et al. 2017). See Data availability section for code, data, and results.

Results

Species' topoclimate distributions

Forest inventory data show that for individual example species (Fig. 3a–c) and the tree flora overall (Fig. 3d), as a landscape becomes colder and/or moister, species occupy microsites that are more south-facing, more windward-facing, and more prominent. Individual species patterns differ from the average for reasons including differences in niche shapes, regional differences in topoclimate effects, and geographic differences in which terrain variables exhibit enough variation to have substantive microclimate effects.

Conceptually, topoclimate effects correspond to the horizontal shifts in these curves. For example, the relationship between northness and high temperature (top center panel of Fig. 3d) implies a difference of ~ 2°C between steep north-facing and south-facing slopes, a value similar to published estimates from microclimate studies (Ashcroft et al. 2008, Bennie et al. 2008, Dobrowski et al. 2013). Note, however, that these marginal summaries cannot be interpreted directly as topoclimate effects due to confounding correlations.

Model evaluation

MCMC diagnostics indicated that the model mixed well, converged properly, and achieved good effective sample sizes (Supporting information). Testing on simulated data showed that the model accurately recovered known parameter values (Supporting information). The model also reproduced the relationships shown in Fig. 3, indicating it successfully captures the key patterns in the dataset (Supporting information).

Validation analyses (Supporting information) revealed that inferred fine-scale bioclimate variables outperform standard macroclimate variables in predicting independent species occurrences withheld from model fitting (Supporting information). This was true even across species boundaries, using bioclimate estimated from one set of species to predict distributions of separate species. Across all 16 variants of the validations, bioclimate outperformed macroclimate to a highly statistically significant degree (all Wilcoxon's $p \leq 1.1 \times 10^{-6}$; Supporting information). The fraction of species for which bioclimate outperformed macroclimate varied from 61.1 to 99.5% across metrics; bioclimate model performance was generally higher for within-sample tests than out-of-sample tests, and for the minimal single-species model than the full multi-species model (Supporting information).

We also found that single-species BISHOP models on average outperformed a standard SDM (fit with the same macroclimate and topographic predictors but lacking the bioclimate interaction term) in predicting species occurrences during cross-validation. Across species, the difference was significant when measuring performance with predictive AUC but not with log likelihood (Wilcoxon's $p = 0.003$ and 0.396, respectively; Supporting information).

Topoclimate effects

For most of the 12 topoclimate relationships, we found strong support for ecologically meaningful effect sizes, as well as major variation in effects across climate zones (Fig. 4).

Northness

Northness strongly influenced tree bioclimate, with north-facing microsites almost universally cooler and wetter than their south-facing counterparts (Fig. 4). A unit increase in northness (equivalent to north- versus south-facing 30° slopes; Supporting information) was associated with up to 43% higher moisture, 3.2°C lower high temperature, and 2.5°C lower low temperature. Northness had its greatest effect on bioclimatic moisture and high temperature in cool–dry regions, and its weakest effect on low temperature in these same regions.

Eastness

Eastness had generally smaller effects than northness (Fig. 4). On average, east-facing microsites were ecologically drier and warmer, with a unit increase in eastness showing up to 11% lower moisture and up to 2.3°C higher high temperature, and with both effects once again strongest in cool–dry macroclimates. Eastness impacts on low temperatures were smaller and more mixed. Combining eastness and northness, we found that in most contexts the three bioclimate variables are maximized in distinct compass directions (Supporting information).

Wind

Windward exposure also showed strong tree bioclimate signatures (Fig. 4). Windward slopes were ecologically drier and warmer than leeward slopes on average, with a unit increase in windward exposure associated with up to 15% lower moisture, up to 0.7°C higher high temperature, and up to 1.9°C higher low temperature. But there was major regional variation, with wind's strongest warming effect on high temperature in cold–dry regions, its strongest warming effect on low temperature in warm–wet regions, and its strongest drying effect in cold–wet regions. In warm–wet regions, windward exposure switched effect directions and had a strong positive impact on moisture signatures.

Importantly, the observed effects of windward exposure could be confounded with the effects of northness and eastness, since prevailing wind patterns mean that windward exposure is often highest on the same southwest slopes that experience maximum afternoon insolation. To explore this issue, we fit a second model omitting windward exposure; it had very similar but slightly larger northness and eastness parameters (Supporting information), which we take to mean that wind–sun correlations are a real but relatively minor driver of our results. This correlation should be kept in mind when interpreting northness and eastness effects as well; it is impossible to fully separate sun- and wind-based phenomena here, although data from other regions could help disentangle them. Fortunately, there is virtually no correlation among northness, eastness, and elevational position, so this issue is limited to windward exposure.

Elevational position

Elevational position within a landscape was also associated with highly context-dependent effects on tree bioclimate (Fig. 4). On average, prominences had drier, warmer signatures than their surroundings, but this varied substantially across climate zones. A site 100 m higher than its neighborhood had ecological moisture levels ranging from 27% wetter to 22% drier, maximum temperatures ranging from 2°C cooler to 3°C hotter, and minimum temperatures ranging from 2.3°C colder to 1.7°C warmer.

Species niches

The final set of model parameters is a three-dimensional bioclimate niche for each species, and we found substantial variation in the position, size, and shape of these niches (Supporting information). We do not elaborate on these results here, as they are not the focus of this paper.

Single-species models

In addition to the full multi-species model, we fit a separate minimal model for each species. There was substantial variation in topoclimate effects across species, but general agreement between the median effect and the results of the full model (Supporting information). Each of three example species exhibited highly credible effects (95% posterior CIs not overlapping zero) for a subset of the 12 topoclimate coefficients (Supporting information).

Comparing each species' topoclimate coefficients to the average temperature and precipitation across its range, we find clear trends across macroclimate gradients for many of the 12 effects (Supporting information). In cases where these relationships are significant (slopes whose 95% CIs do not contain zero, Supporting information), they tend to match the macroclimate trends captured in the full multi-species model (Fig. 4d).

Climate downscaling

We demonstrated the downscaling process by producing 10 m resolution bioclimate variables for an example landscape (Fig. 5, Supporting information). They show much higher levels of fine-scale variation than does a simple interpolation of macroclimate, and 83% of bioclimate values are outside the convex hull of macroclimate values over this landscape (Fig. 5d).

Discussion

This work helps to fill a gap in traditional high-resolution climate modeling approaches, demonstrating that abundantly available species distribution data can be used to infer biologically salient climate patterns at microclimate scales.

Our empirical results illustrate general biogeographic patterns in tree species topographic distributions, quantify strong and regionally variable effects of topography on fine-scale bioclimate as experienced by trees, and enable the creation of high-resolution maps of bioclimate for tree species. Our model validations show that these bioclimate variables better predict out-of-sample occurrences not just for the species used to fit a given model but also for entirely separate tree species (Supporting information), indicating they capture aspects of microclimate variation that are broadly relevant across tree species.

Our results are directly relevant to the North American tree species we used as indicators. Although our species-level cross-validation analyses indicate that these bioclimate inferences often transfer well to tree species not used in model fitting, it should not be assumed that they would extrapolate well to other regions or taxa. For applications in other study systems, it would be necessary to empirically test the utility of these tree-derived variables, or to fit a new BISHOP model to derive bioclimate variables tailored to that system.

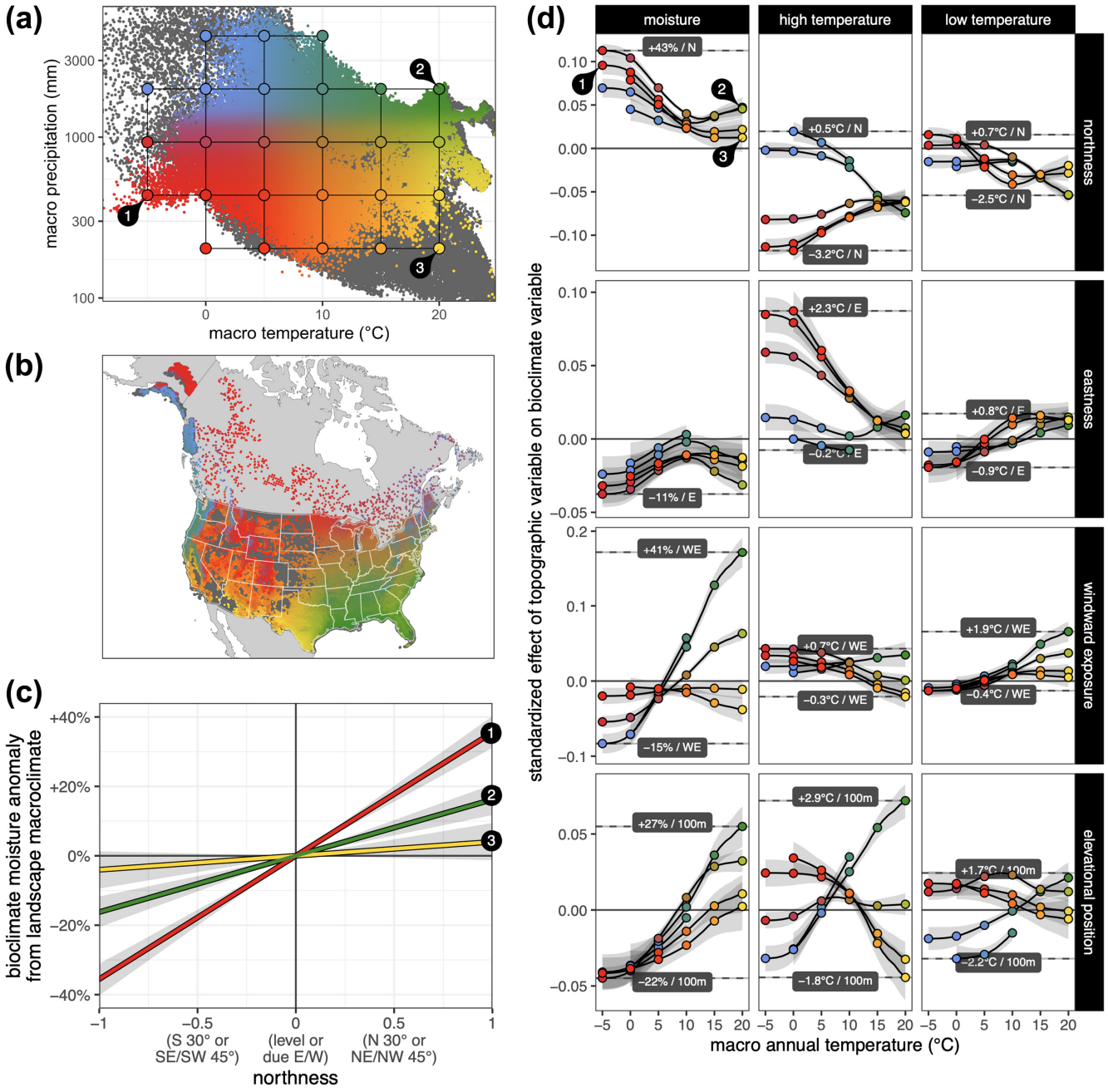

Figure 4. Effects of fine-scale topography on bioclimate, inferred from tree species distributions. (a–b) Macroclimate and location of survey plots, colored by macro-scale temperature and precipitation ('effect modifier' variables in our analysis); colored points are forest plots and dark gray are non-forest plots. The colors correspond to the x- and y-axes of (a), which are then used to illustrate results in the other panels. The reference grid of larger points in (a) corresponds to the points in (d). (c) Examples of inferred northness–moisture relationships under three different macroclimates (annotated no. 1–3 in (a), (c), and (d); x-values represent the northness of a microsite, and y-values represent its bioclimate moisture anomaly (or Δ) relative to macroclimate precipitation, which is assumed to be zero for level sites; the slopes of these lines are the 'topoclimate effects,' which vary across climate zones. (d) Fitted values for topoclimate effects; each y-axis value is the slope of the linear relationship (illustrated in (c)) between the topographic variable listed at top and the microclimate variable listed at right; these effects vary as a function of macroclimate, as indicated by x-axis values and colors. The y-axis shows standardized effects for comparability across variables, while variable-specific units are annotated within each panel (e.g. the reference line in the upper-right panel marked '−2.5°C / N' indicates that low temperature decreases by 2.5°C when northness increases by 1). Lines in (c)–(d) show posterior medians, while shaded ribbons show 95% posterior credibility intervals. As an example to demonstrate interpretation, consider the effect of northness on moisture, depicted in the upper left panel of (d) and further illustrated in (c): the inferred effect (slopes in (c), y-values in (d)) is positive across all climate zones, but greatest in cool–dry macroclimates (red; no. 1), where a unit increase in northness (which equates to the difference between south- and north-facing 30° slopes as seen on the x-axis of (c)) corresponds to a +35% increase in moisture.

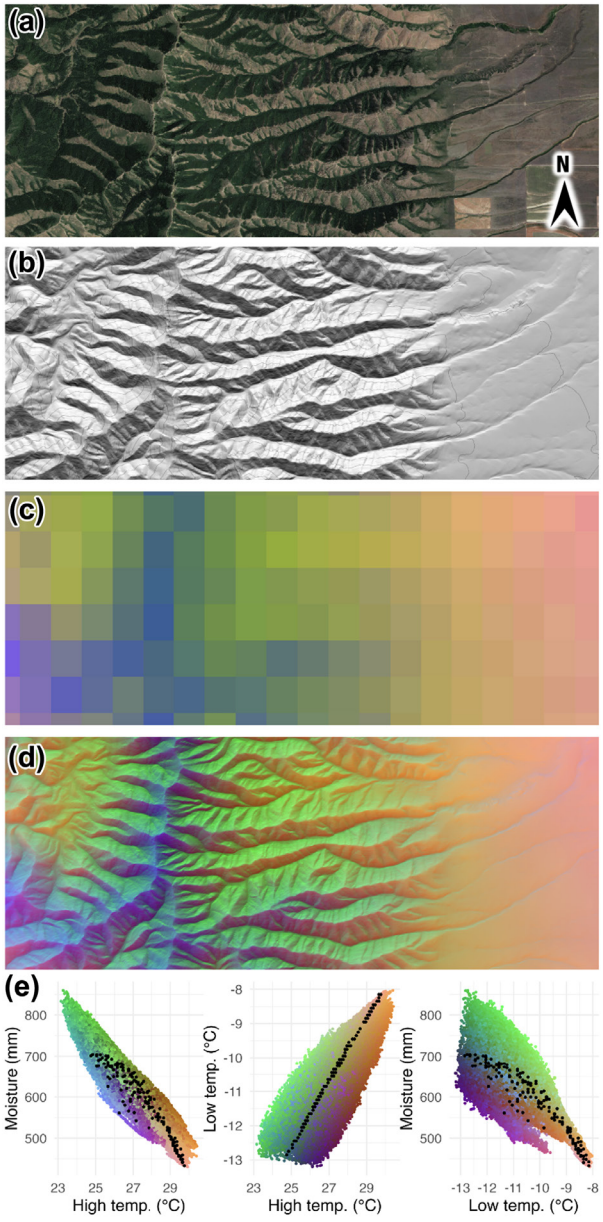

Figure 5. Example of a downscaled 10 m resolution bioclimate map for a rugged 6 × 13 km landscape in southern Idaho, USA, created using the bioclimate inference from species' high-resolution occurrence patterns (BISHOP) model in our analysis. Values represent long-term climate means from 1979 to 2009. (a) Satellite photo of the landscape, from Google Earth, showing the distribution of forest restricted to north-facing slopes and drainages, where microclimates are presumably more suitable; subtler east–west differences are also visible. (b) Shaded relief map of topography across the landscape, based on a digital elevation model with 10 m resolution. (c) Macroclimate data at 1 km resolution, with colors representing unique combinations of high temperature, low temperature, and moisture (i.e. precipitation) as shown in (e). (d) Model estimates of bioclimate experienced by trees, made using (b), (c), and posterior modes from the fitted model parameters from our analysis; colors represent bioclimate as shown in (e). (e) Bivariate scatter plots of climate values across the landscape, with colored points representing bioclimate values from (d) and black points representing macroclimate values from (c).

While bioclimatic inferences built upon tree distributions may not be applicable to other study systems, the BISHOP methodology we introduce could be applied in a range of other domains including for different taxa, physiographic variables, indicator data types, and temporal scales. For example, a study focused on understory plants might use forest structure and soil as physiographic predictors instead of terrain, a study using animal movement data as a bioclimate indicator might downscale sub-hourly weather instead of multidecadal climatologies, or a grassland phenology study might relate terrain to remote-sensed spring green-up dates over an individual season. Even more generally, the notion of a regression model predicting a latent environmental variable that in turn predicts an ecological outcome could have applications beyond inferring fine-scale climate patterns.

Species niches and distributions

While BISHOP was designed principally for inferring bioclimate patterns, not for the traditional SDM goals of inferring climatic niches and predicting species distributions, it is also applicable for those purposes. The niches we inferred for each tree species (Supporting information) are explicitly a function of micro-scale bioclimate rather than macroclimate, and earlier studies have found that similarly derived niche estimates better reflect species' true relationships with climate (McInerny and Purves 2011, Keil et al. 2013). Our results showed that realized macroclimate niche breadths are narrower when controlling for topography than when averaging across it (Fig. 3), suggesting the latter approach would overestimate true niche breadth.

Many prior SDM studies have used terrain variables alongside macroclimate to improve predictive performance. BISHOP demonstrated this same improvement during cross-validation on withheld testing data, performing substantially better on average than SDMs with only macroclimate predictors, and slightly better than SDMs with the same macroclimate and terrain predictors but no latent bioclimate variables. This latter result is not decisive enough to recommend BISHOP over standard methods for studies in which the goal is predicting species occurrences and bioclimate is not of interest for its own sake, but it does suggest that the approach fits the occurrence data relatively well and makes useful SDM predictions.

We note that caution should be taken to avoid circularity that could arise if a BISHOP model were used to predict bioclimate variables, which were then used as predictors in a subsequent SDM. Like suitability predictions, these bioclimate predictions are an SDM output that is not independent of the occurrence data points used in fitting the BISHOP model, which could result in misleading validation metrics if the same occurrence data were used in the subsequent model.

Climate downscaling

Using the fitted model and accompanying R package to downscale macroclimate data, we identified substantial tree bioclimate variation within the example landscape (Fig. 5d). Visually, the downscaled bioclimate data better match the

striking vegetation patterns in this landscape than do the macroclimate data, indicating their likely utility in spatial modeling. In spite of substantial macroclimate variation within this landscape, the large majority of bioclimate values fall outside the observed range of macroclimate values (Fig. 5e), indicating major potential for macroclimate to overlook suitable habitat and to underestimate species persistence under climate change.

Fine-scale bioclimate variables like these could be used in a range of applications requiring data on spatial climate variation, including studies on biogeography, demography, and physiology. As noted above, use of BISHOP-derived bioclimate variables as predictors in subsequent SDMs should be done only with caution, in order to avoid circularity.

While there is no expectation that bioclimate variables like these should precisely match traditional microclimate variables, it would still be informative for future studies to compare the two approaches across different landscapes. Investigating the situations in which bioclimate and microclimate do and to not align could help to uncover important patterns in species climate sensitivity, to identify the microclimate variables most relevant to different taxa, and to identify when bioclimate may be useful as a predictor of microclimate.

Topoclimate effects

Beyond their use for downscaling, the inferred topoclimate parameters themselves reveal how different physiographic features shape bioclimate and how these effects vary geographically, topics that have become a focus for their importance to biodiversity and climate vulnerability (Dobrowski 2011, Moeslund et al. 2013).

Our analysis found that north-facing slopes were almost universally ecologically cooler and wetter than south-facing slopes (Fig. 4), consistent with expectations based on increased insolation on equator-facing slopes. The greatest effects of northness on moisture and high temperature were seen in cool–dry landscapes, perhaps due to factors like greater topographic insolation contrast at higher latitudes (Holland and Steyn 1975) and greater scattering of direct solar radiation in cloudier regions (Dai et al. 1999). In the coolest–wettest climates, the effect of northness on bioclimatic high temperature disappeared entirely, perhaps because persistent moisture in these landscapes leads insolation to drive melting and evaporation rather than raise temperatures (Dai et al. 1999, Dobrowski 2011). The effect of northness on low temperature was weakest in the same cold–dry regions where its high temperature effect was strongest, perhaps due to weaker physical mechanisms (e.g. to snow albedo mitigating warming) or to lower importance of winter minimum temperatures for tree physiology (e.g. because they are dormant and/or cold-hardy) (Nobel and Linton 1997).

Eastness had generally smaller effects than northness, with east-facing slopes warmer and drier than west-facing slopes on average (Fig. 4). Given that micrometeorological studies commonly find the highest temperatures on southwest slopes, which has led to wide use of topographic heat load variables oriented on a southwest–northeast axis (McCune and Keon 2002), our finding that southeast slopes had the hottest–driest signatures may seem surprising. Yet our result is consistent with prior findings that vegetation cover is lowest on southeast-facing slopes in this region (Smith and Bookhagen 2021) and that trees often have slower growth and regeneration on southeast-facing slopes (Kelsey et al. 2018, Redmond and Kelsey 2018). Two factors could drive these patterns: east slopes can genuinely be hotter where cloud cover and precipitation occur predominantly in the afternoon (Geiger et al. 2009), and trees can simply be more sensitive to morning climate than to afternoon climate because they are more physiologically active in the morning (Johnson et al. 2009, Kelsey et al. 2018). Whatever the cause, these findings call into question conventional assumptions about southwest aspects in ecology.

Our results also highlight that the three bioclimate variables each have distinct relationships with aspect (Supporting information), meaning that no individual axis is adequate to describe the multidimensional bioclimate variation found around the circumference of a given hill. This finding is consistent with studies showing that different measures of tree physiology, which are presumably sensitive to different climate variables, reach their maxima on distinct aspects (Stage 1976).

Both windward slopes and locally elevated sites had warmer and drier bioclimates on average, but there was major regional variation in both effects. These results likely reflect the many, often countervailing, mechanisms by which wind and elevational position influence microclimate (Fig. 2). While wind likely drives higher evaporation rates on windward slopes in most situations, it can deliver more precipitation to either windward or leeward hillslopes, and can cause either convective warming or cooling. Compared to depressions, prominences can receive more precipitation but can lose it more quickly due to snow drifting and (sub)surface flow; they are generally windier, which could lead to positive or negative impacts on both temperature and moisture for the reasons discussed above; and they can be cooler due to the lapse rate or warmer due to cold air pooling and reduced shading. Our results demonstrate that the balance among these countervailing phenomena, and/or trees' relative sensitivity to these phenomena, varies across climate zones.

Implications for biodiversity and climate change

Topographically heterogeneous areas are often prioritized in conservation planning because topography generates microclimate heterogeneity (Lawler et al. 2015), which in turn fosters biodiversity by increasing available niche space and reduces local extinction under climate change by generating microrefugia and reducing climate velocities (Loarie et al. 2009, Dobrowski 2011, McLaughlin et al. 2017, Suggitt et al. 2018). Our results help to refine estimates of the relationships between topography and these features of biodiversity maintenance.

We found that each bioclimate variable has distinct relationships with the four topographic variables (Fig. 4). This

means that topography generates multidimensional bioclimate variation within a landscape, which is important because species adapting to climate change face challenges from the need to simultaneously track multiple climate variables changing in different ways (Dobrowski et al. 2013, Hamann et al. 2015, Ordonez et al. 2016).

We also found major variation in topoclimate effects across climate zones (Fig. 4). This implies that identical terrain in different spatial (and perhaps temporal) contexts generates different amounts of biotically relevant microclimate variation. Spatially, this means for example that landscapes in cold–dry regions, which had substantially larger topoclimate effects than cold–wet regions, may see lower tree bioclimatic velocities and more microrefugia as climate changes, per unit of topographic heterogeneity. Temporally, if we apply space-for-time substitution to, for example, the finding that cooler landscapes have steeper northness–moisture relationships, it could imply that the expected degree of bioclimatic moisture heterogeneity within individual landscapes may decline under global warming, reducing their capacity to support tree biodiversity. Further research should investigate how these trends in topoclimate effects shape observed biodiversity dynamics over space and time.

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Author contributions

Matthew M. Kling: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Kathryn C. Baer**: Data curation (equal); Formal analysis (supporting); Investigation (supporting); Software (supporting); Validation (supporting); Writing – review and editing (equal). **David D. Ackerly**: Conceptualization (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Supervision (lead); Writing – review and editing (equal).

Data availability statement

All analyses are based on publicly available datasets accessible from the original cited sources, with the exception of exact FIA and NFI plot locations that cannot be shared for privacy reasons. Results and code are available from the Zenodo Digital Repository: https://zenodo.org/records/11455030 (Kling et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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