

How does incorporating microclimate data into ecological niche models change our estimates of the climatic niche of vascular plant species?

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Abstract

Ecological niche modeling has become a powerful and widely used tool for predicting how species and ecosystems will respond to climate change and for making management decisions related to protecting biodiversity and ecosystem health (Lembrechts et al. 2019). Predictions developed from ecological niche models have also gained recent widespread public attention (Kim 2020) for their large estimates of species extinction rates attributable to climate change (Román-Palacios 2020). Ecological niche modeling has the potential to become an even more powerful tool in our effort to protect the environment from anthropogenic harm, but before we can trust that the accuracy of these models is fit for our purposes, we need to address potentially serious limitations in the ability of ecological niche models which use low-resolution free-air climate data to accurately characterize the ecological niche of species. My research will attempt to examine potential inaccuracies that result from our current ecological niche modeling approach and will hopefully act as a building block for further research that attempts to quantify and correct this inaccuracy. More specifically, I predict that the inaccuracies in our current ecological niche models will trend towards overestimating the niche width of species because low-resolution free-air climate data cannot capture small-scale refugia which may play an important role in some species distributions.

In an attempt to answer this question, I created ecological niche models for several vascular plant species native to the Rocky Mountains using multiple sources of climate data: low-resolution free-air world climate data, free-air climate data from *in situ* sensors, and soil temperature data from *in situ* microclimate sensors. I extracted the same three uncorrelated and biologically relevant environmental predictor variables from each climate data source, and using high-resolution abundance data, created correlative models estimating the climatic niche of each of the focal species. I then compared estimates of the climatic niche width, or the diversity of climate conditions that a species can tolerate, for each species generated from models using the different sources of climate data (Carscadden 2020). I found strongly significant differences between niche width estimates generated from models using low-resolution free-air climate data versus models incorporating high-resolution microclimate. This suggests that ecological niche models which use low-resolution climate data do not accurately characterize the climate niche of vascular plant species. I did not find estimates of niche width from models using high-resolution microclimate data to be consistently narrower than estimates from models using low-resolution free-air climate data, which suggests that microrefugia do not play a dominant role in the distribution of my focal species, and that relationships between free-air and soil temperature are highly complex.

Introduction

The ecological niche of a species describes the range of biotic and abiotic conditions required for a species to maintain a population without relying on immigration from other populations (Polechova 2008). Actual ecological niches are highly complex and multi-dimensional (Blonder 2018), but by identifying the most biologically relevant characteristics of an organism's environment, we can attempt to estimate the distribution of a species in environmental and geographic space. Ecological niche models are becoming increasingly important in understanding the potential impacts of climate change on species and ecosystems (Lembrechts et al. 2019). In conjunction with other biological and environmental information on a species and its habitat, such as environmental and biological constraints on a species geographic dispersal and the rate at which as species can adapt to new environmental conditions, ecological niche models can be used to predict many of the

environmental impacts of anthropogenic climate change such as extinction rates, the amount by which species distributions will shift, and changes in the composition of species found in different ecosystems (Anciães 2006, Pigot 2010, Banerjee 2019).

The accuracy with which ecological niche models can predict the impacts of climate change on species and ecosystems is determined by the selection of environmental predictor variables, the accuracy, resolution, and comprehensiveness of species occurrence data, and the ability of the selected environmental data to characterize the climate conditions experienced by the organism in their habitats (Feng 2019). In areas with complex topography and vegetation structure, one of the greatest limitations to the accuracy of ecological niche models is the lack of available climate data with a high enough resolution to capture small-scale spatial heterogeneity of climate and the high year-to-year variation in climate that is characteristic of most mountainous environments (Lembrechts et al. 2019). In addition, low-resolution world climate data sources estimate free-air climate conditions which can vary considerably from the conditions of near-surface air and soil where the biomass of most organisms is found.

The most commonly used climate data for ecological niche modeling is global weather data interpolated from weather stations measuring free air conditions. This climate data usually has a spatial resolution coarser than 1km and the climate variables extracted from this data are usually averaged over many years or decades (Lembrechts et al. 2019). While this type of climate data might be suitable for ecological niche modeling in flat habitats with little small-scale variation in land cover (Schweiger 2016), significant heterogeneity in topography or vegetation structure has been linked to small-scale soil surface temperature variability of up to 4°C within a 40m² area (Opedal 2015).

Microclimate (i.e. apparent climate) refers to the conditions experienced by organisms in their habitat, and as soon as a habitat can be characterized by a vertical element, or variation in vegetation type or structure, microclimate diverges from the climatic conditions experienced at larger scales (Lembrechts 2019). In mountainous regions such as the Colorado Rocky Mountains, which are characterized by complex topography and heterogeneity in landcover type and vegetation structure, climate varies significantly across short geographic distances and between free air, near-surface air, and soil. The spatiotemporal heterogeneity of near-surface air and soil temperature is rarely incorporated into our current ecological niche models which are used to answer important questions about how organisms will respond to climate change and make decisions related to protecting biodiversity and ecosystem health.

Recently, predictions of climate change driven extinction rates and species distribution shifts derived from ecological niche models have gained widespread public attention because of their grim predictions, but limited academic and public attention has been paid to potential inaccuracies in these predictions that could result from their use of low-resolution climate data products which attempt to estimate free-air climate conditions (Lembrechts et al. 2019). Many of these predictive models are unable to account for the role that microrefugia, pockets of suitable habitat within larger areas of unsuitable habitat, could play in a species distribution (Dobrowski 2011). These models also cannot account for much of the year-to-year or within-season climate variability, such as extreme weather events, which are a characteristic of mountainous terrain.

The goal of my research is to bring this topic more towards the forefront of scientific and public thought, and to shed light on three general topics: how the use of low-resolution free-air climate data could impact the ability of ecological niche models to accurately characterize the ecological niche of species, the importance of refugia in the distribution of species, and which scale-dependent climate effects contribute the most to the formation of refugia and microclimate heterogeneity. I will attempt to provide insight into these topics by measuring whether incorporating microclimate data into ecological niche models impacts our estimates of the climatic niche of vascular plant species living in habitats characterized by a strong vertical element and small-scale variation in landcover, vegetation type, and vegetation structure.

By not capturing the climate experienced at the scale of the organism, and therefore not accounting for the possibility of small-scale refugia as an important driver of a species distribution, I predict that current ecological niche models likely overestimate the climatic niche width of vascular plant species.

Methods

Study Sites. —

Study sites were in the vicinity of sixty-three sites instrumented with soil and free-air sensors installed across the Gunnison Basin in 2019 and 2020 (Figure 1). The soil sensor was a TOMST TMS-4 (Wild et al. 2019) and the free-air sensor was the Onset HOBO Pendant 8K temperature logger. Each TMS-4 microclimate sensor took soil temperature readings at 5 cm below ground level every 15 minutes and each HOBO free-air sensor took temperature readings at 2 m above ground level every hour. Radiation shields were attached to both sensor types to prevent direct radiation from influencing the readings. Problematic climate data resulting from missing radiation caps or dislodged sensors was identified and removed during the analysis stage (see “Cleaning and Summarizing Microclimate Data” below).

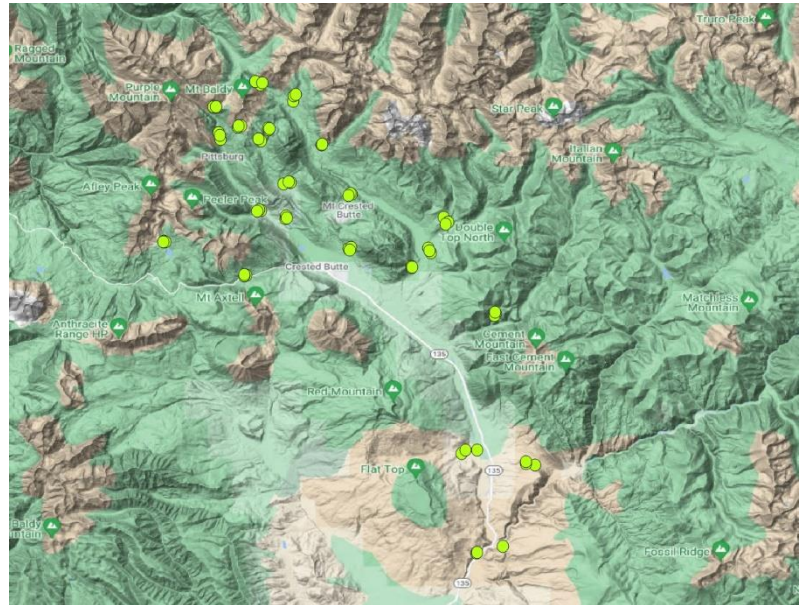


Figure 1. Locations of microclimate sensors in the Gunnison valley. Sensors cover an elevation gradient of ~8,000ft to ~11,300ft. Sensors are set up on ridges, in coves, and in different types of forests to capture a wide climatic gradient.

Focal Species. —

Only a small subset of Gunnison Basin native plant species were potentially suitable focal species for this research. Focal species needed to be abundant enough at the sites to provide an adequate amount of occurrence data and needed to have narrow enough ranges so that their climatic niches could be fully characterized by the available microclimate data. To identify focal species, I made use of occurrence records from iNaturalist and the Consortium of Southern Rocky Mountain Herbaria digital collections. I eliminated all species found above 11,000 ft (3333 m) above sea level and species found at elevations lower than 8,000 ft (2424 m). From the remaining species, I selected the species with the narrowest ranges and highest abundances of herbarium specimens in the RMBL herbarium. The species I selected were *Helianthella quinquenervis*, *Collomia linearis*, *Wyethia amplexicaulis*, *Osmorhiza occidentalis*, *Erigeron flagellaris*, *Eriogonum subalpinum*, and *Potentilla fruticosa*.

Vegetation Sampling. —

To measure focal species abundance, I set up five 1 m² plots at each microclimate sensor. One plot was set up at the location of the microclimate sensor, with the sensor as its center point, and the other four plots were set up 2 m away from the microclimate sensor, in each cardinal direction. Each plot was divided into four 0.25 m² subplots by string and for each subplot I visually estimated the percent cover of each of my focal species (Figure 2).

I used the Daubenmire cover classes (Daubenmire 1959) to estimate the percent cover of each of the focal species found in each subplot. I averaged the corresponding percent cover values for the Daubenmire cover classes for each species for all plots within the site. If I did not find one or more species within the plots,

I systematically searched a 3m radius area around the soil sensor looking for the species. I used a 3m long string connected to the soil sensor to make sure I was searching only within 3 m of the sensor and to make sure that any species I found outside of the plots, but near the sensor was within the 3 m radius before marking it as present for the site. If I did find the species in the site, but outside of the plots, I noted that species as present, but did not estimate its abundance for the site.

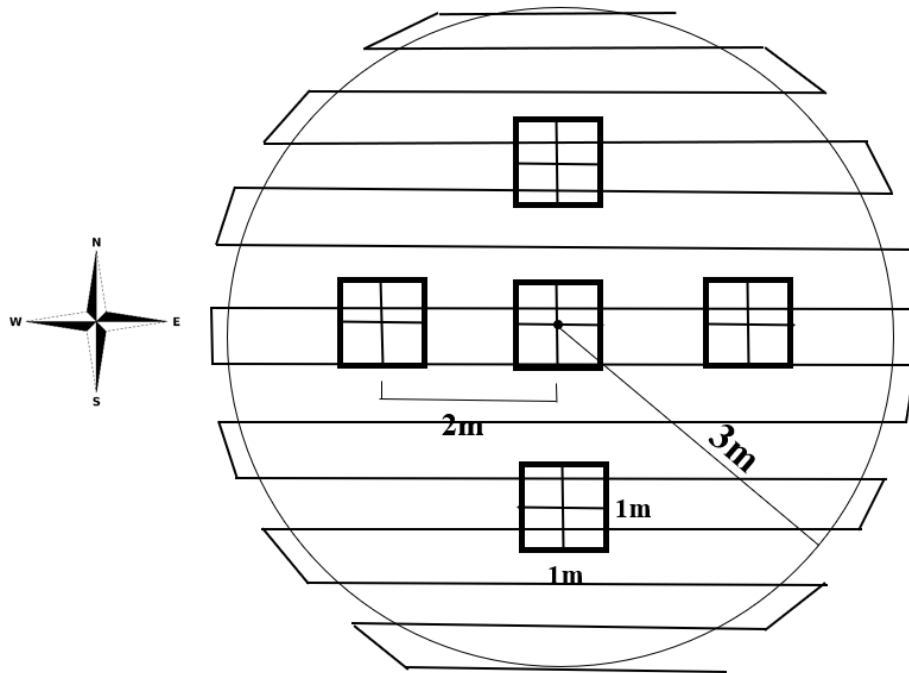


Figure 2. Vegetation survey protocol. Five 1m² plots were set up at each microclimate sensor and used to estimate the abundance of each of the focal species at that site. If any of the focal species were not found within the plots, I systematically searched an area ($r=3m$) around the microclimate sensor, looking for that/those species.

For each site, I assigned each species 1 of 7 possible classifications based on its presence/absence or abundance at the site:

5 – 96-100% plot cover

4 – 76-95% plot cover

3 – 51-75% plot cover

2 – 6-25% plot cover

1 – Trace-5% plot cover

0P – Absent from plots, present in site

0A – Absent from plots, absent from site

Cleaning and Summarizing Microclimate Data. —

To clean the data and merge data for the same site, I used a repository of R code developed by Ian Breckheimer and available at Ian Breckheimer's GitHub page (https://github.com/ikb-rmb/HRL_microclimate). This code identified and removed unusual temperature spikes, values for periods when the sensor was covered in snow or in the lab, and periods of time when the radiation shield had come off or the sensor had been dislodged. In addition, Ian Breckheimer's code created daily summaries for the climate data (daily max temperature, daily min temperature, and daily mean temperature). Using another repository of R code, I created a large number of biologically relevant summaries of the climate data. I create summaries for

several short time periods throughout the year: the 30 days after snow melt, day 30 after snow melt to day 60 after snow melt, May 1st to June 1st, June 1st to July 1st, September 1st to October 1st, October 1st to December 1st, and December 1st to February 1st. For each time period, I calculated mean temperature, 95th quantile and 5th quantile temperature, maximum and minimum temperature, average diurnal temperature, and average daily minimum and maximum temperature. I also used R code to determine the amount of missing data for each time period for each site and excluded climate data for sites for time periods when more than 15% of the climate data for a time period was missing. I used ggplot2 to calculate the amount of correlation between each of my climate summaries and selected three uncorrelated and biological relevant statistics to use in my final analysis.

Statistical Analysis. —

The three climate summary statistics I used for my final analysis were average minimum temperature for the 30 days after snowmelt (Ave_Min_Daily_Var1), 95th quantile temperature for June 1st – July 1st (TopQuantile_Set1) and minimum temperature for December 1st – February 1st (Min_Wint3). Using these climate summaries as environmental predictor variables, I created species response curves for the three focal species with the most non-zero abundance data: *Helianthella quinquenervis*, *Osmorhiza occidentalis*, *Collomia linearis*. I used the mean percent cover for each species at each site on the y-axis of my species response curves. I fitted the species response curves with a generalized additive model using the R package mgcv (version 1.8, Wood et al. 2017).

Biologically driven data alterations were used to ensure that all species response curves were unimodal and met assumptions about ecological niches. Forty pseudoabsence points were added outside of the range of the climate data from the *in situ* sensors. This helped create unimodal response curves for models where there were not enough real absence points at the boundaries of the species climatic niche to create a unimodal response curve. In addition, presence observations were weighted 10x more heavily than absence points based on the assumption that suitable climate is a requirement for a species to be present, but that absences could be attributable to many different environmental variables beyond climate.

I estimated the niche width for each model by subtracting the 90th quantile value from the 10th quantile value estimated from the cumulative area under the species response curve. I subtracted the soil niche width estimate from the free-air niche width estimate to quantify the difference between the niche widths. I used a bootstrapping approach to estimate the amount of uncertainty in the final results attributable to sample size. Significance was based on the percentage of bootstrap estimates showing a difference between the air and soil models different from 0. Differences in niche width were considered significant if greater than 95% of bootstrap estimates were either greater than or less than zero.

Results

As expected, soil temperature varied significantly from free-air temperature within a site across a broad range of temperature summaries. Overall, there was a significant difference in estimated thermal niche width when microclimate data was incorporated into ecological niche modeling.

For *Helianthella quinquenervis*, niche width estimated using soil temperature data was significantly different from niche width estimated using free-air climate data for environmental predictor variables Ave_Min_Daily_Var1 (width difference -2.0570 degrees C, 95% bootstrap interval -2.9317, to -1.2057, Figure 4) and TopQuantile_Set1 (width difference -5.5072 degrees C, 95% bootstrap interval -6.5921, to -4.1364, Figure 4). For both significant results, niche width was narrower for the model that used free-air climate data.

For *Osmorhiza occidentalis*, niche width estimated using soil temperature data was significantly different from niche width estimated using free-air climate data for environmental predictor variables Ave_Min_Daily_Var1 (width difference 2.2252 degrees C, 95% bootstrap interval 1.8623, to 2.6141, Figure 4)

and TopQuantile_Set1 (width difference -5.1703 degrees C, 95% bootstrap interval -5.9688 , to -4.3132 , Figure 4). Niche width estimated using the environmental predictor variable Ave_Min_Daily_Var1 was narrower for the model that incorporated soil temperature data, while niche width was narrow for the model using free-air temperature data when TopQuantile_Set1 was used as the environmental predictor variable

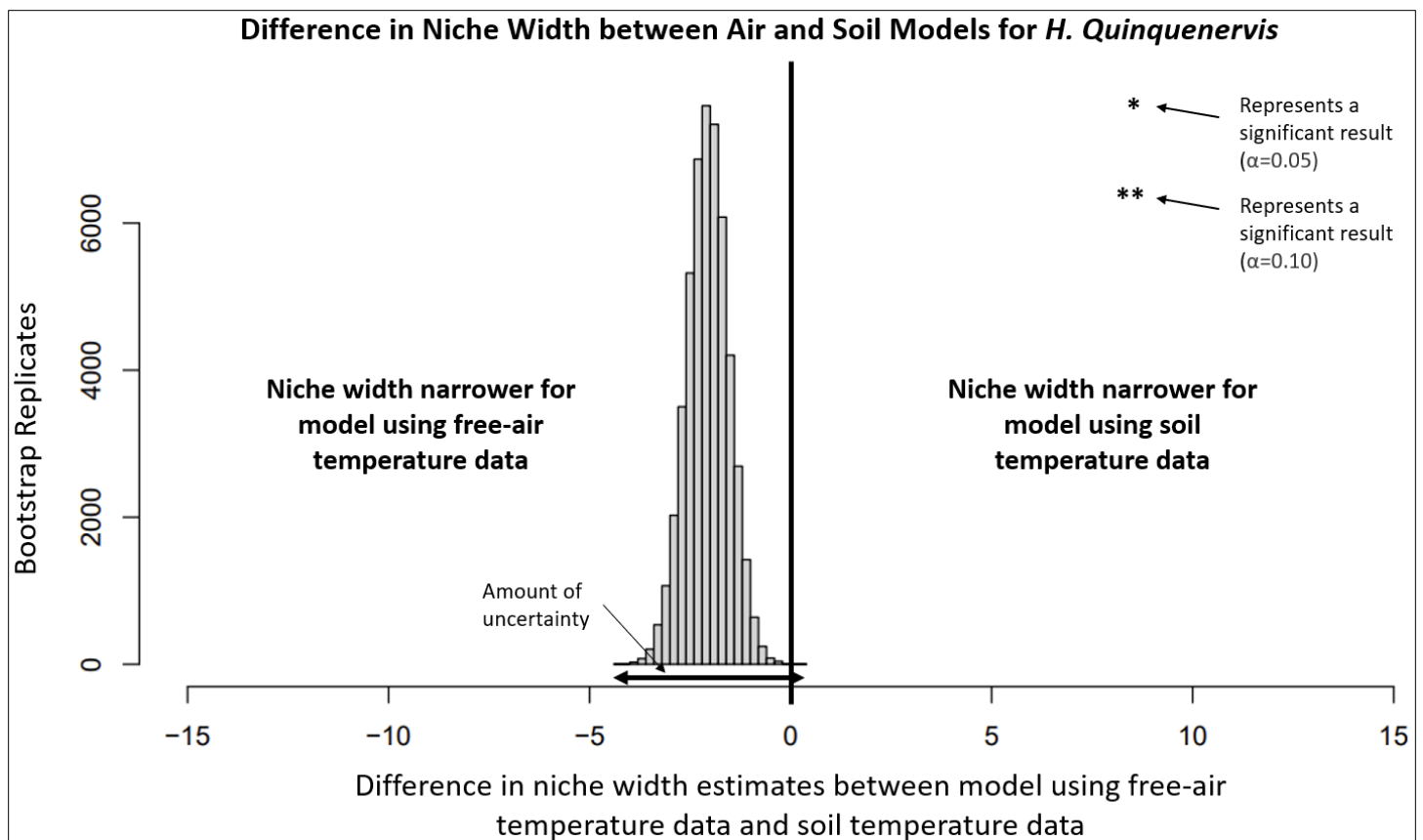
Finally, for *Collomia linearis* there was only a significant difference between niche width estimated using free-air and soil temperature data when TopQuantile_Set1 (width difference 1.8895 degrees C, 95% bootstrap interval 1.2803 , to 2.5300 , Figure 4) was used as an environmental predictor variable. Niche width was narrower for the model using soil temperature data for this environmental predictor variable.

	Niche Width (Air) Mean	Niche Width (Air) (0.05, 0.95)	Niche Width (Soil) Mean	Niche Width (Soil) (0.05, 0.95)	Difference Mean	Difference (0.05, 0.95)	% of estimates greater than 0
<i>H. quinquenervis</i>							
Ave_Min_Daily_Var1	7.3341	6.7514, 7.7962	9.3780	8.6756, 10.0414	-2.0570	-2.9317, -1.2057	0.0001*
TopQuantile_Set1	4.7280	4.3915, 4.9936	10.2192	8.8691, 11.2578	-5.5072	-6.5921, -4.1364	0*
Min_Wint3	7.7730	6.4037, 7.7849	7.0734	6.4037, 7.7849	0.7081	-0.4703, 1.9505	0.83396
<i>O. occidentalis</i>							
Ave_Min_Daily_Var1	3.2551	2.9336, 3.6168	1.0275	0.8715, 1.1836	2.2252	1.8623, 2.6141	0.999988*
TopQuantile_Set1	3.0103	2.7624, 3.3645	8.2045	7.4152, 8.9522	-5.1703	-5.9688, -4.3132	0*
Min_Wint3	2.8853	2.4596, 6.2278	4.8412	4.3249, 5.3434	-1.9064	-2.6205, 1.3875	0.08606**
<i>C. linearis</i>							
Ave_Min_Daily_Var1	5.7668	5.4252, 6.1687	6.3604	5.3068, 7.0368	-0.5618	-1.3538, 0.532	0.17748
TopQuantile_Set1	4.0728	3.5947, 4.5863	2.2017	1.7863, 2.5340	1.8895	1.2803, 2.5300	0.99998*
Min_Wint3	4.2885	3.6736, 4.9980	5.0365	4.4366, 5.5806	-0.7249	1.5734, 0.1727	0.0901**

*Significant ($\alpha=0.05$)
**Significant ($\alpha=0.10$)

Figure 3. Niche width estimates for models using either low-resolution free-air climate data or microclimate data, difference between niche width estimates for models using either free-air or soil climate data, and the percentage of bootstrap replications giving a niche width difference greater than zero. If the percentage of bootstrap replications giving a niche width difference greater than zero is more then 0.50, niche width is narrower for the model incorporating microclimate data. If the percentage of bootstrap replications giving a niche width difference greater than zero is more than 0.95 or less than 0.05, the difference between niche width estimates for the free-air and microclimate models is significant. Ave_Min_Daily_Var1 is average minimum daily temperature for the 30 days after snowmelt, TopQuantile_Set1 is the 95th quantile temperature for June 1st – July 1st, and Min_Wint3 is the minimum temperature for December 1st – January 1st.

A.



B.

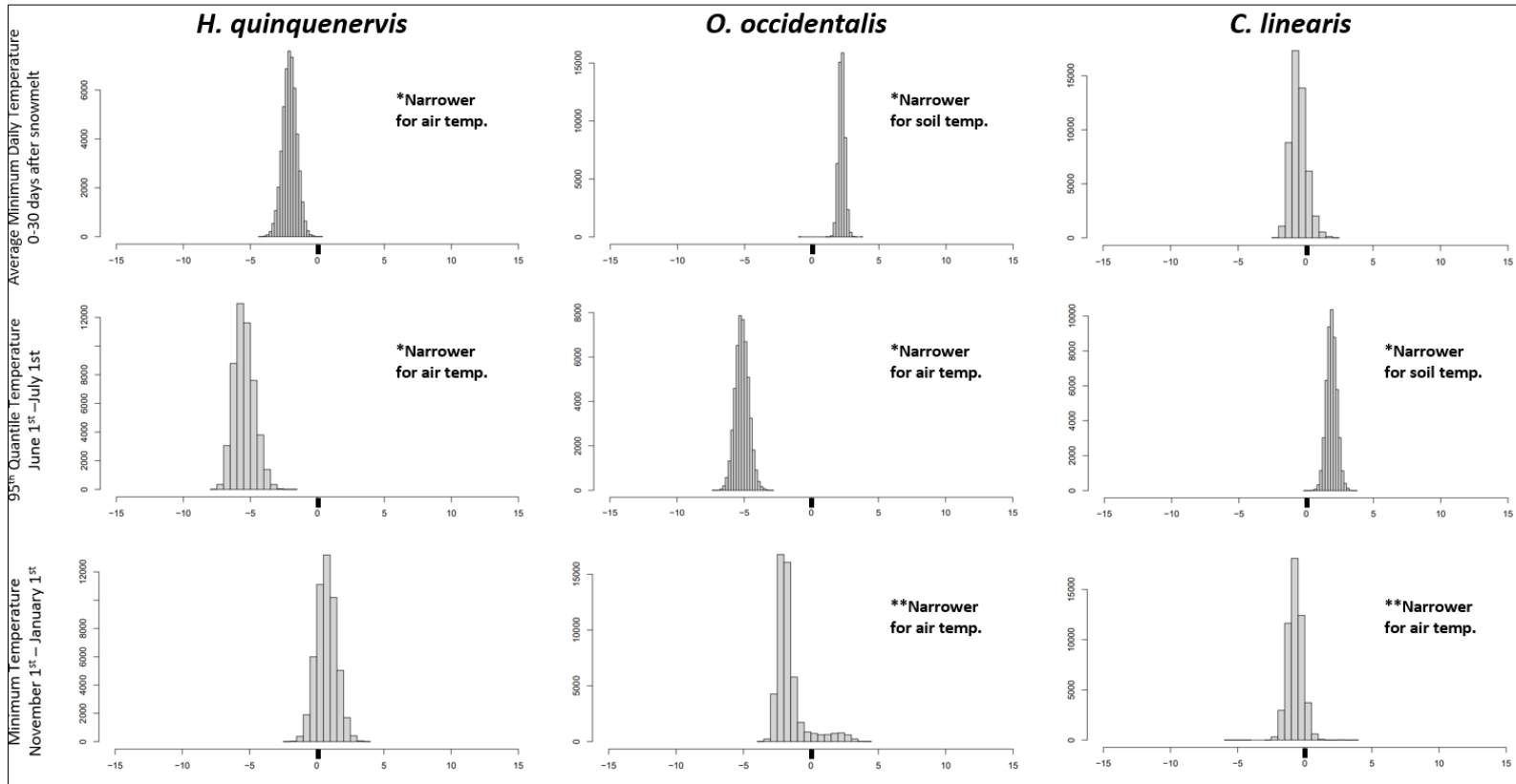


Figure 4. Difference in niche width between models which use low-resolution free-air data and models which incorporate microclimate data. (a). Explanation of how the results are presented in panel B. (b). Results showing estimates of the difference in niche width between models which use low-resolution free-air data and models which incorporate microclimate data from a bootstrapping process.

Discussion

Ecological niche modeling is currently being used as a quick and dirty tool for making predictions related to climate change and for pinpointing strongholds of biodiversity where we can focus our conservation efforts (Miranda et al. 2019), but the ease at which scientists can make use of ecological niche modeling comes with consequences for the accuracy of these models. My research found that species response curves generated from ecological niche models which incorporate microclimate data vary significantly from response curves generated from models using low-resolution free-air climate data. Five of nine combinations of species and climate variables showed strongly significant differences between niche widths estimated using air temperature and soil temperature data. Another two combinations of species and climate variables showed moderately significant results ($\alpha = 0.10$). This suggests that ecological niche models which use low-resolution free-air climate data inaccurately characterize the ecological niche of species. My hypothesis that niche width would typically be narrower for models which incorporated microclimate data was not supported, however, which suggests that small-scale refugia do not play a big role in the distribution of focal species at least for some climatic variables, as well as highlighting the heterogeneity of climate horizontally across geographic space, and the complexity of the relationships between soil temperature, near-surface air temperature, and free-air temperature. My results suggest that ecological niche models which use low resolution climate data probably inaccurately predict the effects of climate change on species and ecosystems. Since ecological niche models are also used to make important management decisions, it is possible that inaccuracies in these models are causing conservation funds to be used inefficiently.

Other research has also found serious inaccuracies in ecological niche models with use low-resolution free-air climate data. Research by Bedia, Herrera, and Gutiérrez found that ecological niche models which use data from WorldClim produced misleading results with poor predictive performance. In addition, they found that these inaccuracies seriously “impaired [the models] practical applicability in biodiversity management and conservation planning” (Bedia 2013).

Even though my results were significant, there are limitations in my own data and analysis approach that should be addressed. First, my sample size for climate and abundance data was limited by the number of microclimate sensors in the Gunnison Basin and the limited abundance of my focal species even within their climatic niche. Problems with the climate sensors also reduced the amount of usable data that I had for analysis. Next, the modeling approach that I used to create species response curves was chosen for its small learning curve, rather than its success at fitting ecological niche models and small sample sizes. Thirdly, my use of data alterations was biologically justifiable, but it could have affected the modeling of my data in unobvious ways. In a future analysis, I hope to improve my analysis approach and use more sophisticated testing procedures to verify the accuracy of my species response curves, and then revise this paper based on the results from that analysis.

Since there is so much heterogeneity in microclimate, and so much complexity in the effects and relationships that determine microclimate, it is hard to imagine that there will be an easy fix for the inaccuracies in ecological niche models resulting from their use of low-resolution free-air climate data. With the recent adaption of remote sensing techniques to ecological research, and with the advancements in techniques used to incorporate remote sensing products into ecological models, it seems like great improvements to the accuracy of ecological niche modeling could be on the horizon. With advancements in remote sensing and climate modeling, we could potentially make interpolated microclimate maps for large geographical areas (Frey et al. 2016, Zellweger et al. 2020). As part of the Rocky Mountain Biological Laboratory’s initiative to develop a state-of-the-art spatial data platform, scientists at RMBL, led by Ian Breckheimer, plan to begin work soon on a microclimate map of the Gunnison Valley using correlative models which relate data from *in situ* microclimate sensors and data from remote sensing products. In order for microclimate data to be of value in ecological niche modeling, the resolution of occurrence data needs to be at least as good as the resolution of the climate data. Remote sensing and machine learning could be adapted to improve the availability of comprehensive and accurately georeferenced species occurrence data.

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