Effects of Terrain on Climate and Consequences for Boreal Songbird Distribution and Refugia

by

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Abstract

Local climates have been increasingly recognized in ecological and climatological studies, particularly because anthropogenic climate change poses threats to biodiversity and ecosystems. Local climates exist at scales of meters to up to a few kilometers and are defined by the set of properties that influence atmospheric conditions at a small scale. These may include biotic properties and topography. Topography and vegetation cover can create thermally heterogeneous landscapes that affect ecological processes and can be strong enough that local climatic trends deviate from conditions at larger (meso or synoptic) spatial scales; this has been proposed as one of the key features of climate-change refugia. Climate change refugia are areas relatively buffered from anthropogenic climate change and have played a role in the historic persistence of species. Identification of these refugia is therefore of considerable importance in light of contemporary climate change. Areas with high refugia potential may warrant greater protection from other sources of human-induced change for conservation purposes (e.g., land-use change, increased wildfire activity). In the western boreal forest, the boreal plains to the east of the Rocky Mountains are marked by limited relief, suggesting limited thermal heterogeneity and refugia potential on the landscape. Despite that, local climate conditions in hills and valley systems favored the persistence of boreal forest in otherwise unfavourable climate for millennia, indicating the potential for refugia at small scales. For forest-associated wildlife, such as boreal songbirds, climate-change refugia is related to the composition and structure of the forests the species inhabit, but also the role that vegetation cover plays in regulating climate at the local scale. Broad-scale bioclimatic models have been used to identify changes in species distribution due to climate change and refugia, but they use coarse resolution or “macroclimate” data that ignore the effects of topoedaphic and vegetation on local climate. Downscaling of macroclimate, which consists of increasing the resolution of climate grids, may be essential in overcoming shortfalls that arise from that and help quantify refugia. Statistical downscaling correlates *in-situ* climate measurements (e.g., subcanopy temperature) with remotely sensed information and topoclimatic metrics and could be a way forward to identify refugia potential driven by local climate across the limited relief of the boreal plains. I sought to determine the degree to which climate varies at small scales (meters to up to a few kilometers) in the western boreal plains and the impacts that local climate has on species distribution and refugia. First, I examined the impact that topography and vegetation cover have on the local climate by sampling climate conditions with temperature dataloggers across a series of hill and river valley systems for several ecoregions in Alberta. I found that summer maximum temperatures (T_{max}) varied nearly 6 ˚C across the elevation gradient sampled. Local summer mean (T_{mean}) and maximum (T_{max}) temperatures in slopes with low levels of potential solar radiation were up to 0.70 ˚C and 2.90 ˚C cooler than highly exposed areas, respectively. T_{max} in incised valleys was between 0.26 and 0.28 ˚C cooler than other landforms, while areas with greater terrain roughness experienced maximum temperatures that were up to 1.62 ˚C cooler. I also found that forest cover buffered temperatures locally, with coniferous and mixedwood forests decreasing summer T_{mean} from 0.23 to 0.72°C, and increasing winter temperature (T_{min}) by up to 2 ˚C. I then applied these results to develop climate offsets to correct and adjust long-term climate predictions for Alberta for local terrain effects (*i.e.*, adjusted climate). I then built four models for the occurrence of 48 songbird species, grouped by their nesting habitat preference, representing all combinations of adjusted vs. unadjusted climate (broad-scale) and climate-only vs. climate + vegetation variables (full model). I applied these models to predict the future distribution of songbirds under a moderate climate scenario to quantify refugia. We observed that the explanatory power of models improved using adjusted vs unadjusted climate for <50% of species. The influence of environmental variables decreased for most groups after replacing unadjusted climate variables for adjusted ones, but climate variables increased importance for coniferous-associated species after adjustment. The amount of refugia area was highest for coniferous-associated species, which also had smaller loss of habitat when using adjusted climate variables in the climate-only model than using unadjusted variables. For deciduous-associated species, loss of suitable habitat was smaller when using adjusted climate regardless of model used. Overall, our results suggest that coniferous-associated species may be more sensitive to local climate conditions, compared to deciduous- and wetland-associated species, which seem to be driven by climate at a regional (or macro) scale. Lastly, I sought to disentangle the role that climate plays directly and indirectly on boreal songbirds, which may inform our understanding of bird responses to climate change in boreal North America. To do this, I used a combination of occupancy models and piecewise structural equation models to investigate the relationship between the occurrence of 16 songbirds to climate, trees and habitat, which allowed me to quantify the direct and indirect limiting factors for songbird occurrence within a single modelling framework. I found a positive relationship between annual climate moisture (potential evapotranspiration – precipitation) and growing degree days (>5°˚C) with occurrence of spruce (*Picea* spp.) trees, 3-4 times larger than the effect of summer precipitation, while T_{min} had consistently negative effects across tree species. I also found that bird occurrence was primarily driven by vegetation characteristics than climate. Coniferous- and wetland-associated species were particularly influenced by spruce biomass. The influence of climate was mostly direct, rather than indirectly mediated through vegetation. For deciduous-associated bird species, vegetation characteristics were more limiting than climate. Relative biomass of spruce trees were the strongest mediators of the indirect effects of climate. Our results suggest that climate change impacts on boreal birds may manifest via direct effects on their resources rather than physiology as well as via indirect effects on vegetation. I conclude that coniferous- and wetland-associated species may be particularly at risk to habitat loss because they may lack the ability to adapt to climate change and be more impacted by climate directly. Coniferous- and wetland-associated species may also be especially at risk because key tree species, such as spruce, may be replaced by fast-growing deciduous trees in the future. I conclude that identification of refugia potential at smaller scales may be crucial for coniferous- and wetland-associated species and may indicate that areas with highest refugia potential could be prioritized for conservation, such as the creation of protected areas.

Preface

This thesis is an original work by César Augusto Estevo.

Chapter 2 of this thesis was published in 2020 as Estevo, C. A., Stralberg, D., Nielsen, S. E., & Bayne, E. (2022). Topographic and vegetation drivers of thermal heterogeneity along the boreal–grassland transition zone in western Canada: Implications for climate change refugia. Ecology and Evolution, 12(6), e9008.

Chapters 3 and 4 of this thesis are being prepared for journal submission.

Dedication

I dedicate this thesis to my wife, Mariana Nagy-Reis. She has been a source of inspiration to pursue a career in biology and research. She has been a real mentor in all aspects of biology and life. I also dedicate this thesis to my parents, Maria do Carmo Zampar Estevo and José Roberto Estevo for believing in me and for valuing education above anything else.

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Your spiritual teachings kept me above the water and gave me air to swim to the shore. You were a career and research inspiration since I met you.

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Chapter 1 – Introduction

The boreal forest is the largest biome on the planet covering more than 1.9 billion hectares (approximately 14% of Earth's land) and spanning more than eight countries (Kurz *et al.*, 2013). The boreal follows the Arctic Circle and represents the northern limit of forested biomes. With that, the boreal is generally defined by low temperatures and dry conditions, particularly in western north America. Given its location farther north, winters are long with long night periods, while summers are a short growing season with long days. This probably led to the perseverance of slow-growing and/or cold-adapted plants, predominantly conifer trees, with occasional lakes and bogs also marking the evergreen landscape (Kurz *et al.*, 2013). Despite being a slow-growing biome, the boreal forest hosts the largest carbon sink on the planet because of slow decomposition and it is estimated that this stores over 25 Pg of carbon in biomass, dead organic matter, and soils (Kurz *et al.*, 2013). This amount of carbon represents 32% of the total carbon stock in the world (Pan *et al.*, 2011).

The modern distribution of the boreal forest is a remnant of changing climate conditions over the last 18 ka BP (kilo annum before present). After the maximum expansion of Laurentide icesheet during the last glacial period, what we describe as "boreal" was in fact distributed as far south as northern Nevada, Utah and Colorado in the United States (about 40˚°N (Dyke, 2007)). As the icesheet retreated northwards, rivers, hills and lakes were formed across Canada. Following suit, the distribution of modern biomes started to form, dictated mostly by temperature and precipitation. In western Canada, the current southern edge of the boreal is marked by a transition zone. Deciduous trees, interspaced by grasslands, predominate this transition zone and is referred to as hemi-boreal or parkland. Further south, prairies are dominated by grassland and fescue. Here temperatures are relatively higher during the summer months and precipitation is very limited, marking a dry landscape (Moss, 1955).

Diverse ecological factors regulate forest structure and composition in boreal forests, making it quite heterogeneous throughout its extent, including temperature, soil physical properties, and moisture (Bonan and Shugart, 1989). In the western boreal, the boreal plains to the east of the Rocky Mountains are marked by limited topography, extreme within annual variations in climate, with long winters, and mild to warm summers (Ireson *et al.*, 2015). Precipitation (and evapotranspiration) are higher in the summer, but a big portion of it falls as snow over the winter, which varies latitudinally. From the southern to the northern edge of the boreal plains, dryness and evaporative demand increase southward towards the hemi-boreal, where summer precipitation is higher. Precipitation as snows constitutes almost half of the precipitation in the north latitudes, and temperatures are cooler (Bonan and Shugart, 1989; Ireson *et al.*, 2015). These climate conditions make the boreal plains the driest boreal ecozone in Canada (Ireson *et al.*, 2015).

The range of the main tree species in the boreal plains is quite defined by moisture, particularly around the balance between precipitation and evapotranspiration (Hogg, 1997). Indices of dryness, such as the Climate Moisture Index (CMI), show that the distribution of spruce trees, or the western boreal at large, are a function of a moist and cool climate. The trailing edge of the boreal plains and leading edge of grasslands corresponds to the hemi-boreal or parkland zone, sharply marked by similar levels of precipitation and potential evapotranspiration. Potential evapotranspiration exceeds precipitation, which marks not only the grasslands ecosystem (Hogg, 1997), but also limit moisture-dependent characteristics and processes, such as the absence of peatlands. The leading edge of the boreal plains in northeast is marked by colder temperatures and permafrost (continuous and discontinuous) (Ireson *et al.*, 2015).

A mosaic of different forest types, wetlands, lakes and grasslands formed as result of geomorphology, hydrology, climate and disturbance in western Canada. Most of the landcover of the boreal plains consists of coniferous forests, followed by deciduous forest and wetlands (fens and bogs). Though topography is limited in the boreal "plains", upland vegetation distribution is determined by elevation and climate at the regional level, while geomorphology, soil texture and topographic position prevail at small scales to influence drainage and water balance (Ireson *et al.*, 2015). Different assemblages of upland forests will emerge depending on regional constrains, but in general upland forests are dominated by white spruce (*Picea glauca*), jack pine (*Pinus banksiana*, in well-drained, sandy and coarse-textured soils), or trembling aspen (*Populus tremuloides*) or a spruce-aspen mixture. Lodgepole pine (*Pinus contorta*) is a major species in the interface between the Boreal and Boreal-Cordillera, but its range extends east as far as central Alberta where hybridization with jack pine has been widely documented and further south in Cypress Hills (Moss, 1955). Peatlands are the most common type of the wetlands, and are formed in lowland, poorly drained flat areas and depressions, wherein the source of inflow water will determine whether bogs or fens are formed, with black spruce (*Picea mariana*) and larch (*Larix laricina*) as the dominant tree species (Ireson *et al.*, 2015). In the grasslands, trees are largely absent and constricted to small patches in areas shaded by topography.

This unique set of climatic and geomorphological constraints that define the boreal plains has led to unique fauna that occupy and rely upon these forests. Birds are the main terrestrial vertebrate species in the boreal. About half of all bird species that occur in the USA and Canada rely on the boreal forest for their survival, with more than 300 species regularly breeding in the boreal region (Niemi *et al.*, 1998; Wells, 2011). Some of these bird species are permanently residents of boreal forests and use it for their entire life cycle, such as Canada's national bird, the Canada jay (*Perisoreus canadensis*). Some birds are short-distance migrants, that spend the boreal winter in temperature areas, while others are long-distance migrants that winter in the tropics. Migratory species are pivotal component in the boreal forest, such that up to 80% of the bird species that breed there are migrants (Niemi *et al.*, 1998). Approximately 96 species of bird in North America can be considered boreal dependent because most of their population (50% or more) breed within the boreal forest (Wells, 2011).

Climate change in the boreal forest

Climate change impacts on ecosystems, including the boreal forest, are an increasing concern. Increasing temperatures over the next century will not only stress the physiology of organisms, but will also likely lead to reshuffling of communities and ecosystems which will lead to habitat degradation and loss in a short timeframe (Stralberg *et al.*, 2009). The boreal forest is expected to experience northward shifts of entire ecoregions (Rehfeldt *et al.*, 2012), with the largest changes in vegetation expected at southern margins where higher evapotranspiration and incidence of drought and heat stress are expected to surpass biological thresholds (Price *et al.*, 2013; Schneider, 2013). Some of this northward shift has already been observed within the last four decades (Berner and Goetz, 2022). For instance, vegetation productivity has increased in the northern boreal margin, and trees have colonized otherwise unforested areas. Meanwhile the southern margin, where conditions are warmest, has actually experienced a decreased productivity and increasing mortality of vegetation greenness, leading to negative trend in greening indices (Berner and Goetz, 2022). The rate at which this expansion is happening is not balanced though, such that loss of boreal biome in the southern margin is faster than tree growth in the north, partially because of the lack of appropriate substrate in northern latitudes, suggesting that boreal biome is in fact shrinking slowly (Berner and Goetz, 2022).

Most changes in the boreal forest will occur because of expected changes in temperature and precipitation. Projections indicate that temperature is expected to increase up to 4.5 ˚C by the end of the century in the boreal plains alone, followed by a moisture deficit during the summer months (Dai, 2013; Price *et al.*, 2013). Such short increase will not come without changes to boreal ecosystem functioning. Forest productivity may in fact increase due to warmer conditions and high atmospheric CO_2, but the same warming may lead to water stress, which would result in productivity loss in areas predisposed to drought, such as the boreal plains (Price *et al.*, 2013). These changes in climate conditions will inevitably lead to detrimental effects for certain plants, either in terms of regeneration of forests and mortality due to water stress, or by an increase in natural disturbances, such as pests, disease, and wildfires. The latter is a key component and major driver of regeneration and species turnover along the boreal plains (Stralberg *et al.*, 2018). Altogether, the anticipated future for the southern margin of the boreal plains and most of the central distribution of the boreal in western Canada is that spruce-dominated forests will be replaced by deciduous trees, interspaced by grassland, which might in fact resemble the parkland zone (Hogg and Wein, 2005). For instance, warming and drying at 10 ka BP in western Canada led to the expansion of the parkland biome northwards, even leading to the contraction of the boreal forest at the time (Dyke, 2007).

In order to keep pace with these changes and maintain its distribution within suitable climate conditions, trees would have to migrate northward or upslope (Hamann *et al.*, 2015). However, in the boreal plains, where extensive flatter landscapes are most common, species will have to migrate greater distances. That is, future analogs of current climate of a given area are located much farther north in flat landscapes because climate velocity, the rate of climate change in space over time, is much higher in flat landscapes (Loarie *et al.*, 2009). Migration is therefore particularly challenging for boreal trees inhabiting the plains because they are slow growing species. Boreal trees take at least 10 years from germination to maturity and seed production (Bonan and Shugart, 1989). When we consider their limited dispersal ability of less than 0.1 km per year (Loarie *et al.*, 2009), most boreal trees will not be able to keep pace with the rate of change of climate (Price *et al.*, 2013). This puts the boreal plains in a particularly vulnerable position in a warming planet and requires climate-smart resource management.

Boreal Climate change and Birds

In niche theory, species ranges can be defined by a suite of macroclimatic conditions that constrain species' physiology (Guisan and Thuiller, 2005). Within a species range, occurrence also depends on climate conditions at finer and more local scales while interspecific interactions and landcover become increasingly important predictors (Guisan and Thuiller, 2005). These conditions at smaller scales, affect vital rates such as recruitment (Briga and

Verhulst, 2015) as well as species energy budgets (Porter, 2002), ultimately leading different populations to be locally adapted (Dunn and Møller, 2019; Anderson and Song, 2020). Climate is therefore an important aspect of a bird's niche. There is growing evidence that extreme weather and changing average climate conditions can directly affect recruitment and fecundity of birds, ultimately affecting population growth and demography (Fisher *et al.*, 2015; Dunn and Møller, 2019). Some aspects of bird migration may also be affected by a warming boreal forest. Migratory species may be negatively affected hard because they rely on environmental queues, such as changes in temperature, to initiate migration. It has been observed that the warming over last few decades has advanced birds migration by a few days already, which leads to mismatch between birds' arrival in their breeding grounds and food availability (Ambrosini, Romano and Saino, 2019). The impacts can also be seen at larger scales, such as in range shifts, and may indicate that thermal tolerance, despite birds' physiological plasticity, has to be considered (Buckley, Hurlbert and Jetz, 2012; Khaliq *et al.*, 2017).

Novel future climate conditions in the boreal forest will inevitably have consequences to inhabiting birds. Population growth of northern population of birds may be disproportionally threatened by climate change because climate is warming at a faster rate in northern latitudes (Loarie *et al.*, 2009), and may be leading their population to growth declines, particularly amongst species that occupy coniferous forests (Virkkala and Rajasärkkä, 2010). The effects have been observed at large scales, where the north margin of boreal species' range is shifting northwards while their southern distribution is contracting (Virkkala and Rajasärkkä, 2011). At the same time, the distribution of species along the south margin of their distribution that are non-boreal obligates is shifting north (Virkkala and Rajasärkkä, 2011), which may eventually increase pressure on boreal species even further through competition. However, the northward expansion of their range is not happening at same rate as their southern margin, indicating that their range may be contracting as a whole. This contraction is likely caused by faster loss of habitat in the south margin of their range due to climate change and lags in vegetation gains in the north (Stralberg *et al.*, 2015a). At the more local and regional scales, the overall rearrangement of entire ecozones that is likely to occur in the boreal plains may also displace coniferous dependent species because of the conversion of coniferous-dominated forests to deciduous-dominated ones.

There are caveats to the negative effects of climate on boreal birds. With increasing temperatures, insect outbreaks and vegetation productivity are expected to increase, at least to some extent. This may mean greater food availability for birds in general, which may counter some of the direct and climate related growth declines in some bird populations. For example, previous spruce budworm (*Choristoneura fumiferana*) outbreaks in the boreal forest have led to a *superabundance* of food at the regional level, which led to an increase in bird density in the short-term (Bolgiano, 2004; Venier *et al.*, 2009). Such positive effects have, however, long-term negative consequences because outbreaks lead to habitat loss by defoliation of spruce trees and stand death.

Resilience of boreal forests and birds to climate change

The persistence of the boreal forest for thousands of years since deglaciation suggest that important attributes of the boreal ecosystem contributed to its resilience, including its capacity to track and sustain itself in locally favorable conditions for growth, despite regionally adverse conditions. For example, the warmer mid-Holocene period was unfavorable for spruce trees in eastern North America. Cooler and moister conditions along the coast, however, served as refugia for spruce trees, which then expanded rapidly at the regional level around 1000 years ago (Schauffler and Jacobson Jr, 2002). Similar phenomena have occurred elsewhere with other taxa during the last glacial period, where some species in the Alps contracted their range into refugia areas during extreme cold period that lasted thousands of years, and then later re-colonized suitable areas once climate became favorable again (Schönswetter *et al.*, 2005; Gavin *et al.*, 2014; Patsiou *et al.*, 2014). Refugia are areas relatively buffered from climate change (Morelli *et al.*, 2016), and played a significant role for the persistence of a number of species historically, which makes its identification of considerable importance in light of contemporary climate change. Refugia have been identified as a prominent ecosystem management and conservation planning solution in the boreal forest and elsewhere (Stralberg *et al.*, 2015a, 2020). For example, refugia identification has been considered as an important step for the conservation of endemic and endangered species (Wilson *et al.*, 2019). In general, however, there is a lack of effective conservation measures in areas with high refugia potential. For example, in North America, only a small fraction of refugia are under formal protection (Michalak *et al.*, 2018; Stralberg, Carroll and Nielsen, 2020), suggesting that the incorporating climate-change refugia is still not considered in conservation planning.

Typically, conditions at local scales can deviate from large scales through a series of processes, some of which can lead to favorable conditions for sensitive species and yield refugia. In the boreal forest, some processes occur at the ecosystem level, where ecological inertia (resistance to external fluctuations) is high enough to buffer climate change (Stralberg *et* *al.*, 2020). Some processes include climate buffering through hydrologic and coastal influences, or even topography and relief, that creates heterogenous climate conditions and cooler than average (Stralberg *et al.*, 2020). Despite the reduced relief in the boreal plains of western Canada, local climate conditions in hills and valley systems favored the persistence of boreal forest in otherwise unfavourable climate. Boreal hills and valley are a result of fluvial erosion of sedimentary bedrock during the Quaternary glaciation (Fulton, 1989. Existing hills systems are upland remnants more resistant to erosion, whereas river valleys are, in general, remains of pre-glacial rivers that were filled with Quaternary sediments (Fulton, 1989). These formations, although small, may have remained climatically suitable and played a role to retain trees in central Alberta during the retraction of the Laurentide Ice Sheet (18–11 ka BP) when ecoregions expanded northward (Dyke, 2007). Cypress Hills, in southeast Alberta, was one of the areas that remained unglaciated throughout the Quaternary period (Fulton, 1989) and retains large isolated remnants of coniferous species (white spruce and lodgepole pine – *Pinus contorta*) in the Canadian prairies because of cooler temperatures at higher elevations (Fulton, 1989).

It is possible that thermal heterogeneity in river valleys and hill systems may result in local climates that are buffered from regional temperature. Relatively cooler (and thus wetter) conditions could be critical for retaining boreal forest tree species during contemporary climate change, especially moisture-limited conifers such as white spruce (*Picea glauca*; Hogg, 1994). Hence, the remaining forest patches could further cool local conditions through canopy shading and associated temperature buffering (De Frenne *et al.*, 2021), which then yields refugia for forest-dependent plant and wildlife species and serve as "stepping stones" to facilitate climate-driven range shifts (Hannah *et al.*, 2014; Stralberg *et al.*, 2015b). However, the value of local processes driving refugia for boreal wildlife in the boreal plains remains uncertain.

Broad-scale bioclimatic models have been traditionally used to identify shifts in species distribution due to climate change (Elith *et al.*, 2006; Lawler *et al.*, 2009; Araújo and Peterson, 2012). However, local climates and habitat conditions are not fully captured by these model projections because of the coarse resolution of climate grids, making it difficult to identify and quantify refugia for boreal species at higher resolutions. In refugia studies, species distribution models (SDM) have been used to identify refugia based on the overlap of current and future projected species range with 'macroclimate' data in coarse resolution (typically 1-10 km) (e.g., Stralberg *et al.*, 2015a; Bateman *et al.*, 2016). There are some shortcomings of macroclimate models, including lower explanatory power (Slavich *et al.*, 2014), overestimation of species' thermal tolerances (Trivedi *et al.*, 2008), and underestimation of species persistence for some species (Randin *et al.*, 2009). Bioclimatic models do have an important role because they provide a reference point to evaluate potential changes in the future distribution of species, but are limited because they do not incorporate important local effects, such as topoedaphic and vegetation impacts on microclimate (De Frenne *et al.*, 2021). For example, different songbird species target different vegetation types for nesting and foraging, and as such species may be differentially susceptible to climate change depending on how much of an impact small scale processes have on the availability of the resources these species require (Duclos, DeLuca and King, 2019).

The advent of low-cost temperature monitoring devices, such as dataloggers (Ashcroft *et al.*, 2012) for *in-situ* measurements, has led to an increase in studies to predict climate at small scales via interpolation (Ashcroft, Chisholm and French, 2008; Slavich *et al.*, 2014), but this approach has limited ability to cover broad spatial extents. Another approach is to combine both the *in-situ* measurements with habitat information to develop mechanistic models of climate (Frey *et al.*, 2016). Topography variables derived from digital elevation models, such as slope aspect and terrain roughness have been used as proxies for microclimate variables and included directly into SDMs (Patsiou *et al.*, 2014), but these variables are static and not projected forward with climate change. Statistical downscaling involves decreasing the grain size of climate grids by correlating *in-situ* climate measurements (e.g., subcanopy temperature) with remotely sensed information or other DEM-derived topoclimatic metrics (Lembrechts, Nijs and Lenoir, 2019). These can then be combined with climate grids available at broad scales to incorporate small-scale forcing factors (e.g., Holden *et al.*, 2016), thus increasing the resolution at which suitable habitat may be predicted. Downscaling is therefore essential in overcoming some of the limitations of macroclimate. I refer to this approach as *climate adjustment* throughout this thesis.

Modelling issues

Circumventing the limitations of large-scale climate predictions with technology and statistics is a promising approach, one of which that allows to understand the different impacts climate might have on species assemblages across scales. For example, the range of the main coniferous tree species of the western boreal forest are driven by moisture balance at broad scales (Hogg, 1994), while within their range, boreal tree occurrence is also influenced by topo-edaphic processes such as soil texture, sand and clay content, pH and surficial geology (Hamel, Bélanger and Paré, 2004). Moreover, topography can directly influence trees when it interacts with climate, such as low exposure from the sun (e.g., north facing aspect), which leads to cooler microclimates that favor the occurrence of heat-sensitive trees. However, birds may be less restricted by climate because of their wide physiological tolerance, suggesting a smaller role of climate variables to delimit their niche (Buckley, Hurlbert and Jetz, 2012). Thus, climate can have distinct direct and indirect effects on their distribution. On one hand, climate affects physiology, limiting birds' energy availability, which is used to maintain their body into their thermoneutral zone (Currie *et al.*, 2004; Buckley, Hurlbert and Jetz, 2012). These effects can manifest in population growth and demography, so changing climate conditions can directly affect recruitment and fecundity of birds (Fisher *et al.*, 2015; Dunn and Møller, 2019). The impacts can also be seeing at larger scales, such as in range shifts (Buckley, Hurlbert and Jetz, 2012; Khaliq *et al.*, 2017). Indirect effects, on the other hand, may influence species distributions by affecting resources, habitat, competitors and nesting habitat (Buckley, Hurlbert and Jetz, 2012; Dybala *et al.*, 2013; Engler *et al.*, 2017; Dunn and Møller, 2019). In this scenario, bird occurrence may be independent of climate, where the latter influences birds via trophic relationships, mediated by vegetation (Buckley, Hurlbert and Jetz, 2012; Ferger *et al.*, 2014). In that way, some environmental factors may be correlated with predictors of bird occurrence, and may not necessarily delimit their niches (sensu Hutchinson, 1957). It is also possible that climate may constrain birds both directly via their physiologically and indirectly via impacts in their habitat. For instance, topographic variation and its associated changes in local climate may not affect bird distributions directly, but it may have strong impacts on landcover, thereby influencing bird habitat suitability indirectly. Climate influences on birds are then an interesting question in ecology because both plants and wildlife are directly affected by climate, while wildlife may also be affected by the impacts of climate on plants. These are particularly important aspects to be considered in the context of conservation and adaptation in a changing climate.

Hence, understanding and teasing apart the direct and indirect impacts that climate may have on wildlife becomes a meaningful question. That is, the indirect process is quite intuitive but hardly quantified in ecological studies. Traditionally, statistical models that seek to answer at least some of these questions use separate models to describe each causal relationship within a natural system. There are a variety of such techniques, including linear and additive models, mixed models (Zuur *et al.*, 2009), and occupancy models (MacKenzie *et al.*, 2002). These are all powerful tools, but they only allow a single response to be evaluated in a causal relationship that need to be interpreted independently. Moreover, indirect impacts cannot be quantified or inferred using these approaches, only hypothesized (Grace, 2006; Lefcheck, 2016). Natural systems are intricately complex, involving multiple causal relationships, where factors can appear both as responses and predictors, whose effects can cascade as the result of a single cause. Simultaneous evaluation of multiple causal hypotheses within a single network is needed to draw a better picture of natural systems. Structural equation models (SEM) has emerged as a technique to resolve multivariate relationships that quantify and tease out direct and indirect effects of interrelated variables (Grace, 2006). SEM consist of using two or more structural equations to model multivariate relationships (Grace, 2006). Structural equations mean that there is evidence that the predictors have a causal effect on a certain response. This technique offers a slight change in perspective from traditional modelling because the starting point is not a null hypothesis, but rather based upon the complete body of evidence and knowledge of a given system and the causal relationships. One of such systems include the expected causal relationship that climate might have on birds and trees and trees on birds themselves. A model is then rejected if observations do not agree with the set of expectation laid out in the model (Grace, 2006).

SEM has received considerable attention in the recent years precisely because of their flexibility and view of natural system as a network of effects, leading to the development of some extension of its modelling approach. Up until recently, SEM were constrained to linear models that use maximum-likelihood to select parameters that best describe variance–covariance matrices. However, in this approach users need to assume that all observations are independent and variables are normally distributed (Grace, 2006). Drawing from graph theory, piecewise SEM (pSEM) solves equations separately, contrarily from simultaneously as the previous approach, allowing for a wide range of sampling distributions (Shipley, 2009). pSEM are followed by tests of directional separation, which tests whether variables are in fact conditionally independent (i.e., there are no missing relationships among unconnected variables Shipley, 2009; Lefcheck, 2016). The implementation of pSEM provides the opportunity to understand the causal relationship between climate, plants and inhabiting wildlife in a single framework, whilst controlling for a multitude of distributional relationships, such presence-absence data from bird surveys.

Summary of thesis objectives

I assessed the degree to which climate varies at small scales in the western boreal plains and the impacts that local climate has on species distribution. My work contributes to our understanding of how limiting topography can yield refugia in an ecosystem endangered by climate change.

More specifically, Chapter 2 examines the impact that topography and vegetation cover have on the local climate. I developed this by sampling climate conditions with dataloggers across hills and river valley systems in several ecoregions in Alberta. I summarized the data collected over a few years in different monthly metric aggregates (e.g., maximum temperature), modelled these metrics as a function of topography and vegetation cover, and compared the results with broad scale climate products (ClimateNA).

I examined the impact that local climate has on species distribution and refugia in Chapter 3. Here, I used the results from Chapter 2 to develop climate offsets, which I then applied to adjust long-term climate predictions for Alberta. I then modelled the occurrence of several songbird species distribution as a function of adjusted or unadjusted (broad-scale) climate variables, as well as other habitat characteristics and predicted their future distribution under a moderate climate scenario to quantify refugia for boreal species. I compared the refugia results based on adjusted and non-adjusted climate variables to understand the role that local climate might have on refugia estimation.

In Chapter 4, I investigated the role that climate plays in defining habitat for boreal trees and, by extension, boreal songbird species. More specifically, I built upon Chapter 2 and adjusted climate variables to local effects of topography. Next, I built piecewise structural equation models to investigate the relationship between the occurrence of songbirds to climate, trees and habitat. This allowed me to quantify the direct and indirect limiting climate factors for songbird occurrence within a single modelling framework.

I conclude my thesis by discussing the most important findings across species groups, while framing the results in the context of climate change refugia, conservation and adaptation in a changing climate.

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Chapter 2 – Topographic and vegetation drivers of thermal heterogeneity along the boreal–grassland transition zone in western Canada: implications for climate change refugia

Summary

Climate-change refugia are areas that are relatively buffered from contemporary climate change and may be important safe havens for wildlife and plants under anthropogenic climate change. Topographic variation is an important driver of thermal heterogeneity, but it is limited in relatively flat landscapes, such as the boreal plain and prairie regions of western Canada. Topographic variation within this region is mostly restricted to river valleys and hill systems, and their effects on local climates are not well documented. We sought to quantify thermal heterogeneity as a function of topography and vegetation cover within major valleys and hill systems across the boreal–grassland transition zone.

Using iButton data loggers, we monitored local temperature at four hill and 12 river valley systems that comprised a wide range of habitats and ecosystems in Alberta, Canada (N = 240) between 2014 and 2020. We then modelled monthly temperature by season as a function of topography and different vegetation cover types using general linear mixed effect models.

Summer maximum temperatures (T_{max}) varied nearly 6 ˚C across the elevation gradient sampled. Local summer mean (T_{mean}) and maximum (T_{max}) temperatures on steep, north-facing slopes (i.e., low levels of potential solar radiation) were up to 0.70 ˚C and 2.90 ˚C cooler than highly exposed areas, respectively. T_{max} in incised valleys was between 0.26 and 0.28 ˚C cooler than other landforms, while areas with greater terrain roughness experienced maximum temperatures that were up to 1.62 ˚C cooler. We also found that forest cover buffered temperatures locally, with coniferous and mixedwood forests decreasing summer T_{mean} from 0.23 to 0.72 ˚C, and increasing winter T_{min} by up to 2 ˚C, relative to non-forested areas.

Spatial predictions of temperatures from iButton data loggers were similar to a gridded climate product (ClimateNA), but the difference between them increased with potential solar radiation, vegetation cover and terrain roughness.

Species that can track their climate niche may be able to compensate for regional climate warming through local migrations to cooler microsites. Topographic and vegetation characteristics that are related to cooler local climates should be considered in the evaluation of future climate-change impacts and to identify potential refugia from climate change.

Keywords: climate change, topography, local climates, refugia, boreal forest, buffering, microclimate

Introduction

The importance and relevance of local climates is increasingly recognized in ecological and climatological studies, particularly in a time where contemporary climate change poses threats to biodiversity and ecosystems (Hannah *et al.*, 2014; Suggitt *et al.*, 2018). Local climates exist at scales of meters to up to a few kilometers and are defined by the set of properties that influence atmospheric conditions at a small scale, including biotic properties (Chen, Franklin and Spies, 1993; Geiger, Aron and Todhunter, 1995; Bailey, 2009), and topography (e.g., aspect and landform; Thornthwaite, 1953; Barry and Blanken, 2016). Local climates are thought to influence aspects of population change and community structure for a variety of organisms and biological processes, including fitness (Hilde *et al.*, 2016), predation (George *et al.*, 2017), genetic diversity (Lampei *et al.*, 2019), and species diversity (Schooler *et al.*, 2020). Despite the potential importance of local climates, our understanding of their relevance to climate-change adaptation in forests and other ecosystems is still limited.

Local climates are dictated by how physical features (physiography) influence incoming solar insolation and wind exposure and, therefore, the energy balance near the earth's surface. For instance, slopes with high sun exposure can show significantly higher temperatures of up to 7 ˚C compared to shaded slopes (Suggitt *et al.*, 2011). Because of changes in airflow across warm and cool slopes throughout the day in mountainous landscapes (Barry, 2008; Barry and Blanken, 2016), prevailing winds can also be more pronounced in rugged terrain, further contributing to temperature differences according to aspect (Williams and Thorp, 2015; De Frenne *et al.*, 2021). Likewise, phenomena such as cold air pooling in valleys may create temperature inversions, thus decreasing local temperatures drastically (Nielsen and Haney, 1998; Daly, Conklin and Unsworth, 2010). Interestingly, thermal differences driven by physical features may lead to differences in temperature with the same order of magnitude as the projected effects of climate change globally (Daly, Conklin and Unsworth, 2010; Nevo, 2012).

The extent to which terrain drives local climates varies widely. Local influences can be such that local climate is buffered from regional averages (Dobrowski, 2011). In other words, terrain effects can be strong enough that local climatic trends deviate from conditions at larger (meso or synoptic) spatial scales; this has been proposed as one of the key features of climate-change refugia (Dobrowski, 2011; Morelli *et al.*, 2016; Stralberg *et al.*, 2020). Consequently, local topography can create thermally heterogeneous landscapes that directly affect key ecological processes and patterns (Swanson *et al.*, 1988; e.g., Elsen *et al.*, 2020) and have the potential to reduce the exposure of biodiversity to climate extremes (De Frenne *et al.*, 2013; Letten *et al.*, 2013; Scheffers, Edwards and Diesmos, 2013; Wolff *et al.*, 2020). For instance, thermal heterogeneity was critical for the redistribution of many species during and after the last glacial period, particularly for disjunct populations (e.g., Fuentes-Hurtado, Hof and Jansson, 2016; Leipold *et al.*, 2017), suggesting the importance of refugia for species in a contemporary climate-change context. Therefore, refugia - areas that are “relatively buffered” from contemporary climate change (Morelli *et al.* 2016) - can provide “safe havens” for organisms against climate change (Sears, Raskin and Angilletta, 2011; Keppel *et al.*, 2012).

Vegetation may also influence local atmospheric conditions. For instance, forest cover can act in synergy with topography to influence radiation balance locally, thus affecting temperature, humidity and wind, and generally resulting in cooler local climates within the understory (Vanwalleghem and Meentemeyer, 2009). Old-growth forests with high biomass and complexity can buffer maximum temperatures by 2.5 ˚C relative to forests with simpler stand structure (Norris, Hobson and Ibisch, 2012; e.g., plantations; Frey *et al.*, 2016), and can be about 5 ˚C cooler than areas with less forest cover (Davis *et al.*, 2019). Meanwhile, forest canopies retain heat in the winter, resulting in warmer temperature under the canopy relative to non-forest areas, especially in boreal regions (De Frenne *et al.*, 2019). Thus, forests can buffer local climates against both extreme warm and cold temperatures.

Local climates have been investigated extensively in mountainous regions and mountain basins, where topographic effects (from varied terrain and elevation) are most pronounced (e.g., Cantlon, 1953; Clements, Whiteman and Horel, 2003). In mountainous areas, local changes in elevation provide excellent “natural experiments” for ecological and meteorological studies, with a diversity of gradients, including radiation, humidity, precipitation, and temperature. Elevation differences had also been used to identify climate-change refugia (Ashcroft *et al.*, 2012). However, elevation *per se* is a poor predictor of climate at smaller scales because air temperatures near the ground may not be correlated with temperatures in the free atmosphere (Lookingbill and Urban, 2003; Dobrowski, 2011). This suggests that temperature predictions that are solely based on temperature changes with elevation (adiabatic lapse rates) do not include important topographic and vegetation effects on local climatic conditions. Therefore, incorporating finer-scale features such as aspect, landform and forest cover can substantially improve our predictions of the local climate.

In landscapes with gentle terrain, thermal heterogeneity and seasonal attenuation of minimum and maximum temperatures (i.e., climatic buffering) should be more limited compared to mountainous landscapes, as the strength of influence of topographic factors should be smaller (e.g., Keppel *et al.*, 2017). The velocity required for organisms to track their climate niche as the climate changes is also greater in flatter areas, relative to mountains where climatic gradients are steeper, suggesting that flatter areas might be more susceptible to rapid changes in climate (Loarie *et al.*, 2009; Carroll *et al.*, 2015; Barber, Nielsen and Hamann, 2016). In the boreal plains region of Western North America, thermal heterogeneity in river valleys and hill systems may result in local climates that are buffered from regional temperature increases. Relatively cooler (and thus wetter) conditions could be critical for retaining boreal forest tree species, especially moisture-limited conifers such as white spruce (*Picea glauca*; Hogg *et al.*, 1994). The remaining forest patches could further cool local conditions through canopy shading and associated temperature buffering (De Frenne *et al.*, 2021). The resulting refugia can provide habitat for forest-dependent plant and wildlife species and serve as “stepping stones” to facilitate climate-driven range shifts (Hannah *et al.*, 2014; Stralberg *et al.*, 2015).

The boreal forest is expected to experience northward shifts of entire ecoregions (Rehfeldt *et al.* 2012), with the largest changes in vegetation expected at southern margins where higher evapotranspiration and incidence of drought and heat stress are expected to surpass biological thresholds (Price *et al.*, 2013; Schneider, 2013). In much of the western prairie province of Alberta, Canada, the difference between precipitation and evapotranspiration is close to zero, resulting in the potential for local differences in vegetation. In the prairie part of the province, patches of trees consisting of species typically associated with boreal forests persist along north-facing slopes in river valleys and at higher elevations (Figure 1.1). Most notably, the Cypress Hills of southern Alberta contain one of the few larger isolated remnants of coniferous species (white spruce and lodgepole pine – *Pinus contorta*) in the Canadian prairies because of cooler temperatures at higher elevations. These forests were likely established during the retreat of the previous ice sheet when boreal mixedwood forests occupied much of what today are the grassland landscapes of southern Alberta (Moss, 1955; Strong and Hills, 2005; Dyke, 2007). These ecological remnants provide contemporary analogs for what northern boreal forest landscapes may resemble in a warmer and drier future. Therefore, we view boreal forest refugia as areas in which topographic effects lead to cooler local climates that allow coniferous trees, particularly white spruce, to persist over time.

We sought to understand the role that fine-scale variations in local topography and vegetation play in promoting thermal heterogeneity. Moreover, we wanted to quantify the degree to which topography and vegetation can reduce or buffer temperatures in the boreal-grassland transition zone of Western Canada. Specifically, we investigated the effects of different terrain features (including elevation) and vegetation cover types on minimum, mean and maximum monthly temperatures during summer and winter seasons, when extreme temperature values are most likely. We defined temperature buffering as some combination of decreasing mean and maximum temperatures during summer warm months, increasing mean and minimum temperatures during winter cold months, and/or decreasing temperature ranges in both seasons. In addition, we investigated the extent to which a standard gridded climate product – based on interpolated weather station data and downscaled as a function of elevation-derived lapse rates – captures thermal heterogeneity. We did so by monitoring and analyzing climate conditions in several river valleys and hill systems along a 1000+ km latitudinal gradient in Alberta, Canada. Our survey design covered vegetation ranging from isolated boreal forest remnants within landscapes currently dominated by grassland in the south to contiguous boreal conifer and mixedwood forest in the northern reaches.

Methods

Site selection and study areas

This study encompassed four hills and 12 river valleys systems along a latitudinal gradient in Alberta, Canada that covers a transition from boreal forest to parkland to grassland ecosystems (Figure 1.2). The parkland natural region is a transition between grassland and boreal forests and consists primarily of aspen (*Populus tremuloides*) and grassland mosaic interspersed with occasional balsam poplar (*Populus balsamifera*) and white spruce forests (*Picea glauca*). Hill and valley formations in Alberta are a result of differential fluvial erosion of sedimentary bedrock in the Western plains during the Quaternary glaciations. Existing hills systems are upland remnants more resistant to erosion, whereas river valleys are, for the most part, remains of pre-glacial rivers that were filled with Quaternary sediments (Fulton, 1989). Such pre-glacial valleys are prominent in northern regions of Alberta, particularly in between boreal highlands (Figure 1.2). With the retraction of the Laurentide Ice sheet (18 – 11 ka), ecoregions and biomes that were once pushed farther south expanded northwards (Dyke, 2007), with some vegetation remaining along climatically suitable areas in central Alberta. Cypress Hills, in southeast Alberta, was one of the areas that remained unglaciated throughout the Quaternary period (Fulton, 1989). We sampled similar upland vegetation across hill and valley systems, which consisted mostly of white spruce, trembling aspen, birch (*Betula* spp.), and balsam poplar, as well as plains cottonwood (*P. deltoides*) in valley bottoms of southern sites. The Cypress Hills site (farthest south and considered part of the Rocky Mountain natural region in Alberta) also included lodgepole pine (*Pinus contorta*). Some valleys were treeless on south-facing slopes, creating a sharp contrast with forested north-facing slopes (Figure 1.1).

Figure 1.1: Examples of ecosystems and contrasting slopes sampled in Alberta, Canada. Writing-on-Stone Provincial Park with a tree patch at valley bottom (bottom; ~49° N); contrasting slopes with remnant conifer forests in river valley systems at Dry Island Buffalo Jump Provincial Park (center left) and Tolman Badlands Heritage Rangeland Natural Area (center right) in South-Central Alberta, Canada (~52° N); hills systems at

Marten Hills (top left) and Watt Mountain (top right) in Central (~55˚ N) and Northwest (~59˚ N) Alberta, respectively.

Normal climatic conditions in our study sites vary widely. At colder and wetter sites in the north (55˚ N through 59˚ N), mean annual temperatures ranged from -2.7 to 1.4 ˚C (30-year normal; 1961 – 1990), and precipitation ranged from 256 – 281 mm per year. The central and southern regions (49˚ N through 55˚ N) experienced long dry and hot periods during summer and warmer temperatures during winter. In central Alberta, mean annual temperatures at study sites ranged from 1.6 to 2.7 ˚C and precipitation from 386 to 432 mm. In the southmost river valley sites, the mean annual temperature was approximately 5 ˚C and mean annual precipitation hovers around 315 mm. In Cypress Hills, the southernmost hill system, the mean annual temperature was slightly cooler and precipitation slightly higher (~2.5 ˚C and 435 mm, respectively).

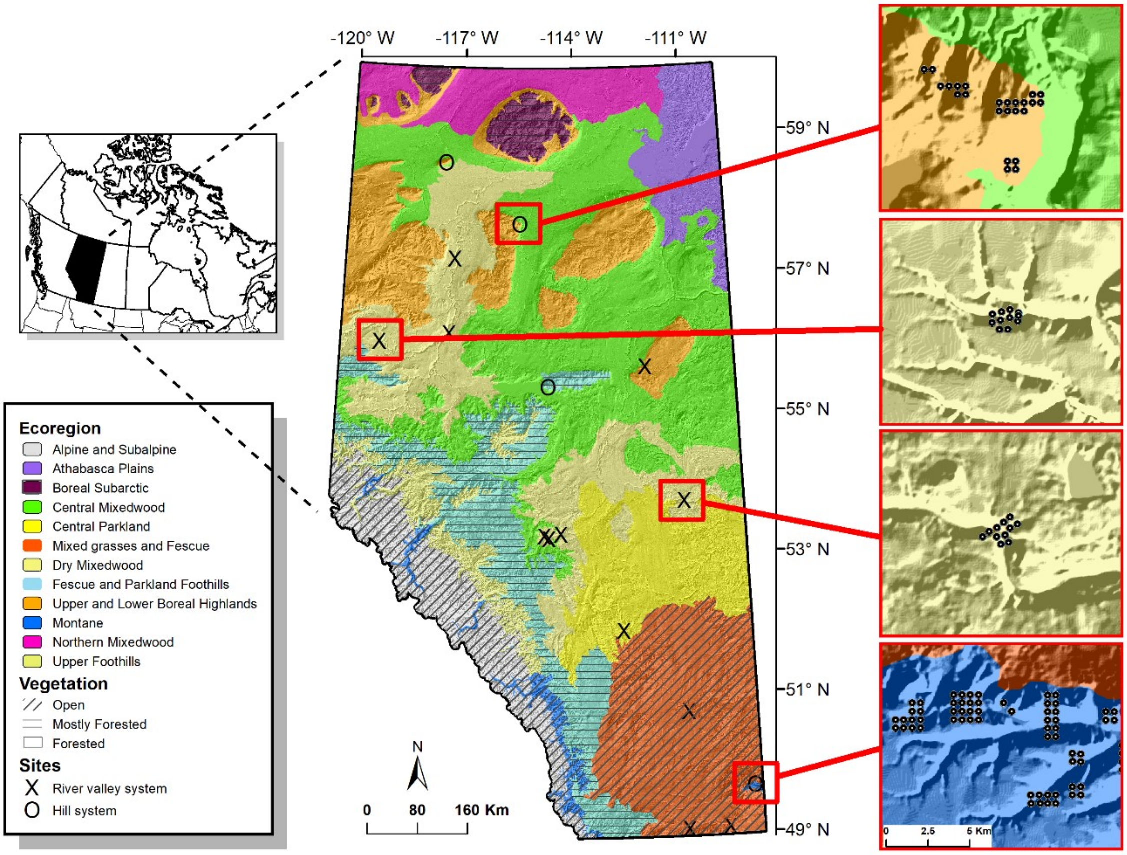


Figure 1.2: Location of sample sites (river valley and hill systems) in Alberta, Canada with different sub-ecoregions in the province. Some classes were grouped for mapping. Northern portions of Alberta are often composed of open wetlands interspaced

by trees; therefore, this simplified version may not necessarily represent entire sub-ecoregions. The map is overlaid on a hillshade model to depict topography across study sites. Column on the right depicts examples of sampling scheme of some iButtons (black dots) in some valleys and hills systems.

Current differences in mean annual temperature in Alberta are approximated by changes in latitude (inverse relationship) along the boreal-parkland-grassland gradient (Figure S1.1). We identified four mean annual temperature strata (hot-warm-cool-cold) within Alberta and selected accessible hill and valley systems (i.e., up to 5 km of a road) within each stratum for field sampling along the boreal-parkland-grassland gradient. We avoided the Rocky Mountain foothills, which are much wetter and less seasonal than boreal environments, and also contain different floristic communities. We selected sites mostly within protected areas to reduce confounding factors caused by human activities (i.e., forest clearing). Once we identified hills or valley systems, we placed iButton temperature data loggers (details below) at a spacing of at least 500 m along elevational gradients by either setting up transects along the elevation gradient or by placing a 500 m virtual grid over the area with iButtons at the junctions of the grid. We attempted to achieve equal coverage of distinct landforms, i.e., ridgetops, valley bottoms, and slopes with large aspect contrasts (i.e., northeast- and southwest-facing), reflecting differences in solar radiation. We purposely selected river valleys that were representative of the existing distribution of trees in river valleys of the sites in the grasslands ecoregion. For instance, sites in the far south (~49° N) were either treeless or contained trees only in valley bottoms (Figure 1.1, bottom). In the grassland ecosystem (mixed-grasses and fescue biomes) and central parkland, patches of trees were more common in valley bottoms and generally occurred on north-facing slopes (Figure 1.1, center left and right). Further north in the boreal and central mixedwood biomes ecosystems, trees were present throughout (Figure 1.1, top left and right).

Temperature data logger deployment and sampling

We deployed 283 iButton temperature data loggers (Thermochron iButton model DS1922L; N_{Hills}= 166 and $N_{Valleys}$= 117) between May and June 2014 (hill systems) and 2018 (river valleys), with some river valleys stations deployed in September 2018. We programmed iButtons to sample every 90 min and retrieved them approximately one to three years after deployment (July/August 2015 – Watt Mountain [~59 °N] and Buffalo Head Hills [~58 °N]; May/June 2016 for Cypress Hills [~49.5 °N]; June/July 2017 for Marten Hills [~55 °N]; and

August/September 2020 for river valleys). 14 iButtons from hill systems and 29 from river valleys either failed or were damaged by wildlife, leading to a final sample size of N = 240. For each iButton, we built inexpensive radiation shields following the procedures of Holden *et al.* (2013). Radiations shields have been reported to be comparable with weather stations, with a small warm bias of up to 1 ˚C (Holden *et al.,* 2013; Terando *et al.*, 2017). This allowed us to compare temperatures from data loggers directly with weather station-derived estimates, such as ClimateNA (see details below). We attached each shield, with its enclosed iButton, to the north-facing side of a tree at 1.5 m from the ground or to wooden stakes approximately 1.5 m above the ground in treeless areas. We removed obviously unrealistic iButton logger values (high and low), i.e., where temperature sensors failed, by excluding values outside of ± 3 times the interquartile range for all summer months. This allowed us to use only reliable temperature measures and thus remove bias in our analysis since all metrics were summarized to monthly averages. We discarded data for the month of deployment or retrieval for sampling stations if it had less than 20 days of sampling. We imputed daily temperature data for the stations that had missing days by using univariate time series imputation with spline interpolation within the *imputeTS* package in R (Moritz and Bartz-Beielstein, 2017). This approach allowed us to estimate monthly temperature metrics in a way that respected the seasonality of a given month (e.g., colder temperatures at the end of a summer season).

Temperature metrics

Following Suggitt *et al.* (2011) we calculated five temperature metrics from the raw data for each month: average of daily maximum (T_{max}), minimum (T_{min}), and mean temperatures (T_{mean}), growing degree days above 5 ˚C ($GDD_{5)}$ and average of daily temperature range (T_{range}). In addition to these metrics, we also calculated the 99th percentile of daily maximum temperatures (T_{99}) to evaluate topographic effects on extreme temperature events. We chose these metrics based on their relevance to several ecological processes, such as animal and plant thermoregulation, plant recruitment, animal distribution, and because of their relevance in identifying climate change refugia from a temperature standpoint (Dobrowski, 2011; Ashcroft *et al.*, 2012; Briga and Verhulst, 2015). Our next step was to subset the data into two seasons consisting of data from June, July, and August (northern hemisphere summer season), and December, January, and February (winter season). These two seasons are ecologically relevant for several reasons. The summer period is crucial for several taxa as it corresponds to the growing season for plants and the breeding season for most animals. In addition, the effects of climate change are expected to be more pronounced during summer, with higher maximum temperatures and more extreme drought periods, but also during winter, with higher minimum temperatures and increased frost-free periods (Price *et al.*, 2013). We gave particular attention to T_{max}, T_{99} and GDD_5 for the summer season as these metrics are more directly driven by the warmer season, while we calculated T_{mean} and T_{range} for both summer and winter, and T_{min} for the winter (refer to the appendix for results of all metrics in both seasons). Such an approach allowed us to consider our results in view of the buffering effects that forest cover and terrain could have on local climates (i.e., lower summer T_{max} and T_{mean} and warmer winter T_{min}; De Frenne *et al.*, 2019). The summer temperature metrics considered here are particularly relevant from a boreal refugia perspective because of their direct linkage to conditions that could be favorable (cool and wet) or unfavorable (hot and dry) to seedling development and recruitment of coniferous trees, especially white spruce (Hogg, 1995; Price *et al.*, 2013). Therefore, in analyzing the effects of topographic variables on local climates we focused on coniferous boreal trees, especially white spruce.

Finally, we calculated the correlation between temperature metrics to assist with model interpretation.

Topographic and vegetation variables

We used a suite of topographic and vegetation variables that could affect climate conditions at the local scale: solar radiation, topographic roughness index (TRI), landform, elevation, latitude, compound topographic index (CTI), and vegetation cover (Table 1.1). Topographic variables were calculated from a 50-m digital elevation model (DEM) derived from 1:50,000 Topographic Data of Canada (CanVec series).

Table 1.1: Topographic and vegetation variables used in temperature regression of temperature sensors deployed in hills and river valley systems in Alberta, Canada

Category	Variable	Definition	Related literature/Source
Topography	Elevation	Derived from a 50 m DEM	
	Solar Radiation	Based on nonparametric multiplicative regression using slope, aspect and a	(McCune, 2007)

		constant latitude of 53 N	
	Landform	Valley or ridge top based on topographic position index of a 300 m radius and a slope grid	(Jenness, 2006)
	TRI	Topographic roughness index, as the sum change in elevation in the eight neighboring cells	(Riley, Degloria and Elliot, 1999)
	CTI	Compound topographic index, calculated based on flow direction, accumulation and slope derived from a 50 m DEM	(Rho, 2002; Nielsen, Boyce and Stenhouse, 2004)
Vegetation	Forest Cover	Percentage of forest cover around each iButton station on a 3x3 50 m pixel moving window	(ABMI, 2010)

We estimated annual potential relative solar radiation (in MJ/cm^2/year; hereafter solar radiation) by using a multiplicative kernel smoothing technique that uses slope, aspect, and cumulative warming from the afternoon sun following equations from McCune and Keon (2002) and McCune (2007). Despite not being a direct measure of solar radiation, this modeled terrain-based estimate should reflect the effects of slope and aspect on local climates. We decided to use a constant midpoint latitude in this case so that we could model the effects of latitude separately in our models (see Analysis section).

We calculated the terrain roughness index (TRI) as the sum of the change in elevation between a given grid cell and its surrounding cells, which indicates the level of topographic heterogeneity in a certain area (Riley, Degloria and Elliot, 1999). The compound topographic index (CTI) tracks the flow of water drainage and could be used as a proxy for cold air drainage, soil moisture, and topographic evenness (Lookingbill and Urban, 2003; Daly, Conklin and Unsworth, 2010; Dobrowski, 2011). We calculated CTI by using the spatial analyst extension in ArcView 3.2 and a script developed by Rho (2002). To generate landform classes, we first calculated the topographic position index (TPI) using a circular radius of 300 m and a slope raster to generate landform grids further categorized into 10 classes (Jenness, 2006). For this study, we extracted whether the station was located at an incised valley or ridge top by using the first and last class generated when calculating landform. We grouped the other classes into a single one, as their effect is likely represented in the other topographic variables. For vegetation, we summarized forest cover from the spatial landcover inventory layer developed by the Alberta Biodiversity Monitoring Institute (‘Wall-to-wall Land Cover Map’ version1.0 from 2010 retrieved from http://www.abmi.ca, ABMI, 2010). We extracted broadleaf, conifer and mixedwood polygon layers from the land cover map and rasterized them to a 50-m resolution. We used a moving window of 3 x 3 cells to calculate the percent cover of vegetation in the surrounding landscape. We used these same layers for mapping purposes and comparison with ClimateNA (see analysis part below). Collinearity was not an issue with these covariates, as all the variables in our analysis had reasonably low correlations (Pearson $R^2 < 0.7$, Figure S1.2) and were all included in our analysis.

Analysis

Effects of topographic factors and vegetation on local climate

We used three different approaches to evaluate the effects of topography and vegetation cover on the local climate. First, we standardized all variables to facilitate the assessment of effect sizes. We compared a set of *a priori* models and hypotheses (Table 1.2) with different variable combinations using the Akaike Information Criterion to rank models for small sample size (AICc; Burnham and Anderson, 2004). Our main objective was to evaluate the amount of support for models that included only elevation against models that incorporated additional topographic and vegetation effects. Thus, all models in this step include elevation as an environmental null model. The *aspect model* was used to evaluate the importance of differences in solar radiation associated with slope and aspect. With the *topodiversity* model, we wanted to know whether roughness and topographic diversity were important, while the *topodiversity and vegetation effects* models also included the percentage of broadleaf, conifer and mixedwood canopy cover around the station as an additive effect. The *moisture and landform* model was used to test the level of support for the potential effects of soil moisture and topographic position based on CTI and landform classes. Here, we emphasized models for summer T_{max} and T_{mean}, and winter T_{mean} and T_{min} (please refer to the appendix for models for all metrics in both seasons). We included latitude in all models to control for the overarching influence of latitude on temperature.

Secondly, we developed full models with additive effects for all variables mentioned in the previous section to develop spatially explicit predictions to compare with another gridded temperature product (ClimateNA; see details in the next section). We evaluated the significance, direction and strength of influence of β coefficient estimates to interpret the effects of each covariate on the variation of local temperature. We used general linear mixed-effect models with the monthly temperature metrics as response variables for all models. We developed separate model sets for the winter and summer seasons and fit models using each hill or river valley system as a random intercept to account for latent climatic phenomena and properties of each system. We added an additional random effect for the year and month of sampling. We also incorporated a within-group correlation structure to account for temporal autocorrelation within each season by using a continuous autoregressive process (corCAR1) and a constant variance function structure with month as a grouping factor. We performed all modelling within the R environment (R Core Team, 2013) using the *lme* function from the *nmle* package (Pinheiro *et al.*, 2007) for linear mixed effect models.

Table 1.2: Models developed to compare different effects of local topographic features and vegetation cover on different temperature metrics and related hypotheses. All models also included latitude as an additional variable (see Analysis section).

Model	Variables	Mechanism	Hypothesis	Expectation
Elevation	Elevation	Adiabatic cooling	Adiabatic lapse rates (i.e., elevation) are the predominant factor regulating temperature in hills and valleys	Decrease in temperature with increasing altitude; expected negative effects across temperature metrics
Aspect	Solar radiation	Increased/decreased solar radiation	Heating from incoming solar radiation due to aspect and terrain slope lead to warmer local climates in highly exposed slopes, and cooler local climates in areas with low exposure	All temperature metrics are expected to increase with increasing sun exposure. Conversely, topographic shading has a lower temperature. T_{range} is expected to increase
	Elevation	Adiabatic cooling		Decrease in temperature with increasing altitude; expected negative effects across temperature metrics
Topodiversity	Solar radiation	Increased/decreased solar radiation	Terrain ruggedness, through increasing air motion and mixing, and incised valleys,	All temperature metrics are expected to increase with increasing sun exposure; shaded areas are cooler

Model	Variables	Mechanism	Hypothesis	Expectation
	Elevation	Adiabatic cooling	through cold air pool, are cooler, while ridges are warmer; aspect and slope lead to warming (high exposure) and cooling (low exposure). Local climates are highly heterogeneous	Decrease in temperature with increasing altitude; expected negative effects across temperature metrics
	Landform	Temperature inversion and cold air pooling		Incised valleys are expected to have lower T_{min} and T_{range} as a result of cold air pooling, while ridge tops are warmer.
	TRI	Air motion and mixing		Lower temperatures are expected in highly rugged areas
Moisture and Landform	Elevation	Adiabatic cooling	Soil moisture potential and drainage leads to different local climates; valleys are colder, while ridges are warmer due to cold air pool formation and exposure, respectively	Decrease in temperature with increasing altitude; expected negative effects across temperature metrics
	CTI	Drainage and wetness		Wetter areas (i.e., high soil moisture potential) are expected to have higher T_{min} and lower T_{max}/T_{99};
	Landform	Temperature inversion and cold air pooling		Decrease in temperature with increasing altitude; expected negative effects across temperature metrics
Topodiversity and Vegetation Effects	Solar Radiation	Increased/decreased solar radiation	Local climates are highly heterogeneous, driven by roughness (air motion), solar exposure and landforms (e.g., cold air pools and exposure); local climates below forest canopies are more moderate, with lower daily variability	All temperature metrics are expected to increase with increasing sun exposure; shaded areas are cooler
	Landform	Temperature inversion and cold air pooling		Incised valleys are expected to have lower T_{min} and T_{range} as a result of cold air pooling, while ridge tops are warmer
	TRI	Air motion and mixing		Lower temperatures are expected in highly rugged areas
	Elevation	Adiabatic cooling		Decrease in temperature with increasing altitude; expected negative effects across temperature metrics
	Vegetation	Canopy buffering		Canopy cover is expected to decrease T_{max}/T_{99}, increase T_{min}, and decrease T_{range}. Coniferous cover is expected to have stronger effects (i.e., cooler)
Full	CTI	Drainage and wetness	Topographic diversity and local vegetation (Topodiversity and	Wetter areas (i.e., high soil moisture potential) are expected to have higher T_{min} and lower T_{max}/T_{99};

Model	Variables	Mechanism	Hypothesis	Expectation
	Solar Radiation	Increased/decreased solar radiation	Vegetation Effects hypothesis), in addition to soil moisture potential (Moisture and Landform hypothesis), create highly heterogeneous thermal landscapes	All temperature metrics are expected to increase with increasing sun exposure; shaded areas are cooler
	Landform	Temperature inversion and cold air pooling		Incised valleys are expected to have lower T_{min} and T_{range} as a result of cold air pooling, while ridge tops are warmer.
	TRI	Air motion and mixing		Lower temperatures are expected in highly rugged areas
	Elevation	Adiabatic cooling		Decrease in temperature with increasing altitude; expected negative effects across temperature metrics
	Vegetation	Canopy buffering		Canopy cover is expected to decrease T_{max}/T_{99}, increase T_{min}, and decrease T_{range}. Coniferous cover is expected to have stronger effects (i.e., cooler)

Finally, we calculated conditional and marginal coefficients of determination (the proportion of variance explained by fixed and random effects, R^2_c, and fixed effects only, R^2_m, respectively) to examine the goodness-of-fit of our models using the *squaredGLMM* function in the *MuMIn* package (Nakagawa and Schielzeth, 2013; Barton, 2020). We also evaluated the improvement in the explanatory power of models that incorporate all topographic variables (*full model*) relative to the *elevation* model by measuring the percent change in R^2_c.

Mapped local climate and comparison with ClimateNA

We used the full models based on iButton data from step two in the previous section, but with non-standardized variables, to generate spatially explicit predictions of summer T_{mean} and T_{max}. We then constrained our mapped predictions to a region of approx. 25 x 25 km around each river valley or hill system, thereby avoiding predicting outside the range of our data. To illustrate our results based on iButtons and to compare with other gridded products, we also created climate grids using ClimateNA, a graphical user interface package that provides climate predictions at different scales (Wang *et al.*, 2016). The interface provides data in different temporal scales (e.g., monthly, yearly, seasonally) when provided with either point coordinates or a raster DEM. The package uses monthly temperature data for the normal period of 1961 –

1990 as a baseline, which is compiled from four different sources depending on the region. For Alberta, it resamples PRISM grids to a 4 km resolution baseline by using bilinear interpolation and empirical lapse-rate with high accuracy (Wang *et al.*, 2016). For recent years, ClimateNA retrieves historical climate data generated by the Climate Research Unit at the University of East Anglia, which is updated yearly. Comparing ClimateNA to our iButton predictions is advantageous as the former provides scale-free climate estimates and empirical lapse rates that should be consistent with the ones in our iButton predictions. We generated spatial temperature estimates with ClimateNA (version 6.3) for the same 25 x 25 km region and same sampling period as the iButtons (2014 – 2020) by supplying the ClimateNA software with a DEM at 50 m resolution. We then extracted monthly average temperature data from ClimateNA for the same location, month and corresponding year of iButton data. Even though iButtons and ClimateNA predictions differ in terms of precision and range of values, the difference between the two rasters should remain constant across elevational gradients in the absence of topographic effects. However, the dissimilarity should be higher at valley bottoms, mountain tops and in areas with high or low incoming solar radiation, which are factors that are not necessarily captured by interpolated products. Therefore, our goal was to quantify the underlying drivers for the expected difference between ClimateNA and direct iButton readings. We quantified the magnitude of the difference between ClimateNA and iButton measurements as the absolute difference between ClimateNA grid cell values extracted and the iButton measurement for that station (summarized as monthly T_{max}, T_{min}, GGD_5 and T_{mean} averages). We modelled the absolute difference as a function of the full model from Table 1.2 for the summer and winter seasons but included an interaction term between solar radiation and the percentage of vegetation cover to account for warmer and treeless slopes. We used the same random effect and correlation structure from the models detailed in the previous section and evaluated the effect size and significance of each variable in explaining the differences. Finally, we generated temperature surfaces based on ClimateNA and iButtons for July 2018 and calculated the absolute difference between the two data sources for illustrative purposes.

Results

Effects of topographic factors and vegetation on local climate

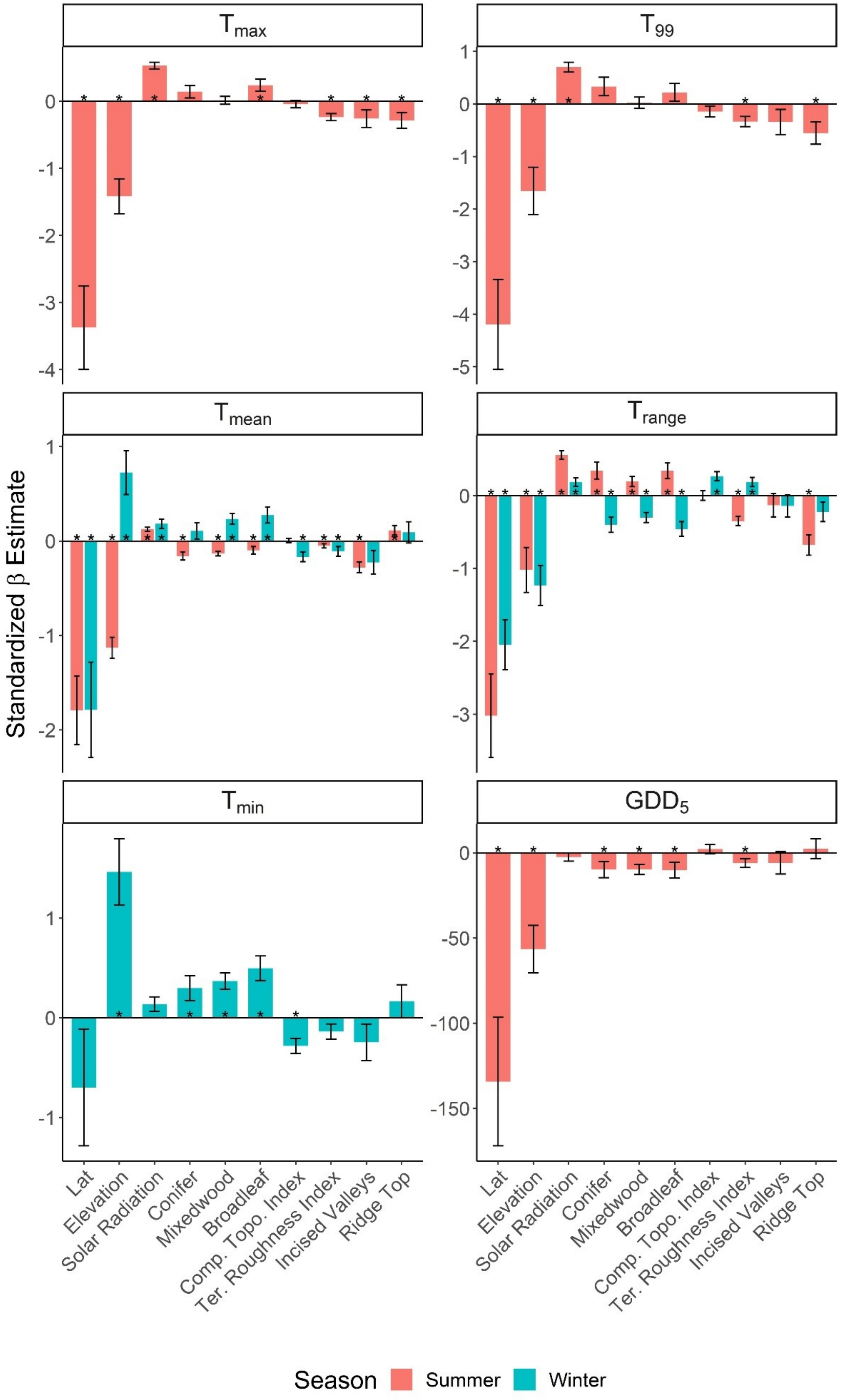
Models that included all predictor variables (*full* model) were among the top three models in both summer and winter for all metrics (Table 1.3), and were always among the models with the most support (ΔAICc < 2), except for summer T_{range} and winter GDD_5 (see Table S1.1), Models that accounted for tree cover, solar radiation, topographic roughness and landform variables, in addition to latitude and elevation (i.e., the *topodiversity and vegetation* *effects* model), received either similar or more support than the full model for most metrics in both seasons. Overall, models that included additional topographic features, besides elevation, received substantially more support than elevation-only models in both seasons. However, adding a terrain wetness term (i.e., CTI) did not improve models substantially and the *Moisture and Landform* model received little support throughout the analysis. Notably, the correlation between temperature metrics within seasons was high (R^2>0.7, Figure S1.3) for most metrics, except for summer T_{min} (R^2<0.7) and in some cases for T_{range}. In most cases, the ranking for the full model was similar, but the level of support could vary substantially. For example, summer T_{max} and summer T_{range} were strongly correlated, but the support for the full model was ΔAICc<2 for summer T_{max} and ΔAICc>2 for summer T_{range} (Table S1.1), suggesting that topographic and vegetation effects on summer T_{range} are largely driven by their effects on summer T_{max}.

Table 1.3: Model ranking for two different temperature metrics for the summer months between 2014 and 2020 in river valley and hill systems in Alberta, Canada. Only the top three models are presented for T_{max} and T_{min}. Please refer to Table 1.2 for variables in each model. K – number of parameters, ω – weighted AICc of the model, LL – negative log-likelihood. ΔAICc – difference in AICc between a given model and the top model of that model set.

Season	Metric	Model	K	ΔAICc	ω	LL	R2m	R2c
Summer	T_{max}	Topodiversity and Vegetation	17	0.00	0.55	-2451.64	0.39	0.84
		Full	18	1.42	0.27	-2451.32	0.39	0.84
		Topodiversity	14	2.28	0.18	-2455.86	0.39	0.84
	T_{mean}	Topodiversity and Vegetation	17	0.00	0.73	-1469.74	0.37	0.95
		Full	18	1.99	0.27	-1469.71	0.37	0.95

		Topodiversity	14	24.29	0.00	-1484.96	0.34	0.95
Winter	T_{mean}	Full	18	0.00	0.99	-2095.69	0.18	0.91
		Topodiversity and Vegetation	17	8.54	0.01	-2100.99	0.18	0.91
		Topodiversity	14	26.18	0.00	-2112.91	0.16	0.91
	T_{min}	Full	18	0.00	1.00	-2487.68	0.11	0.85
		Topodiversity and Vegetation	17	12.03	0.00	-2494.73	0.11	0.85
		Moisture and Landform	13	19.26	0.00	-2502.46	0.09	0.84

The direction of each variable's effect remained relatively consistent across all temperature metrics and seasons (Figure 1.3, Figure S1.4). In terms of the effect size of each variable relative to elevation, we found, as expected, that latitude was the strongest individual predictor for most metrics, except for winter T_{min}, for which elevation was the strongest (positive) predictor. Other topographic and vegetation variables had a smaller influence on temperature metrics when compared with elevation. For instance, solar radiation increased summer high temperature extremes (T_{max} and T_{99}) and temperature range (T_{range}), with a combined effect size that was approximately 37 – 54% of the effect size of elevation. Aspect- and slope-driven increases in solar radiation also increased summer mean temperature (T_{mean}), but with a smaller effect (~25%). Overall, the directionality of effects was similar over the winter, but with lower magnitude.



T_{max}
T_{99}
T_{mean}
T_{range}
T_{min}
GDD_5
Standardized β Estimate
Lat
Elevation
Solar Radiation
Conifer
Mixedwood
Broadleaf
Comp. Topo. Index
Ter. Roughness Index
Incised Valleys
Ridge Top
Season
Summer
Winter

Figure 1.3: The influence of topographic and ecological variables over the monthly average of daily T_{max}, T_{min}, T_{mean}, the 99th percentile of daily maximum temperatures (T_{99}), growing degree days above 5 ˚C (GDD_5) and average of daily temperature range (T_{range}) for the summer and winter seasons in river valley and hill systems in Alberta, Canada. Standardized beta coefficients are from the full model (refer to the Methods section and Table 2 for more details). See Figure S1.4 for results of other temperature metrics. Error bars represent standard errors and * indicates significant estimates at α=0.05.

Terrain roughness (TRI) significantly decreased high temperature extremes (T_{max} and T_{99}), mean temperatures (T_{mean}), and the range of temperatures (T_{range}) during the summer, but its effect size was much smaller than that of elevation (~4 – 24%). Our proxy for soil wetness had no effects on summer temperature but decreased minimum and average temperatures and the range of temperatures in the winter to a minor degree. Summer temperature decreased significantly in incised valleys, particularly for T_{mean} (~ 25% of the effect size of elevation).

Overall, the amount of surrounding forest cover for all three types had significant negative effects on most summer temperature metrics, except for high extremes (T_{max} and T_{99}), where broadleaf cover had even positive effects (Figure 1.3 and Figure S1.4). The effects of vegetation cover on winter temperatures were positive for T_{min} and T_{mean}, suggesting a buffering effect. Out of the three different vegetation types analyzed, coniferous forest cover had the strongest (negative) effect on average summer temperature (T_{min} and T_{mean}), particularly compared to broadleaf forest.

In absolute terms, summer T_{max} varied ~6 ˚C across the elevation gradient sampled. Relative to areas with low exposure, areas with high solar radiation increased summer maximum temperatures by 5.66 ˚C, or even up to 7.46 ˚C for T_{99}. This meant that summer T_{mean} and T_{max} on steep, north-facing slopes with lower levels of potential solar radiation were up to 0.7 ˚C and 2.9 ˚C cooler, respectively, than highly exposed areas (Figure 1.4). Incised valleys were between 0.26 and 0.28 ˚C cooler than other landforms, while terrain roughness decreased T_{max} and T_{99} by about 0.03 to 0.04 per index unit, up to 1.62 ˚C. Areas fully covered by broadleaf, coniferous, or in particular mixedwood forests experienced significantly lower summer T_{mean} than unvegetated areas by about 0.23 ˚C, 0.37 ˚C, and 0.72 ˚C, respectively (Figure 1.4). Over the winter, all forest cover types increased T_{min}, particularly under mixedwood (2.01 ˚C) and broadleaf forest cover (1.16 ˚C). Elevation had a strong warming effect in winter T_{min} with an increase of up to ~5.50 ˚C, relative to low elevation areas. Interestingly, we found that the strength of forest cover was similar to that of topographic factors, particularly for T_{mean}, T_{min} and T_{range}. Figure 1.4 summarizes predicted effects for T_{mean} for July of 2018, which was a typical year in terms of temperature for Alberta (see Figure S1.5 and Figure S1.6 for unstandardized coefficients of all metrics in both seasons).

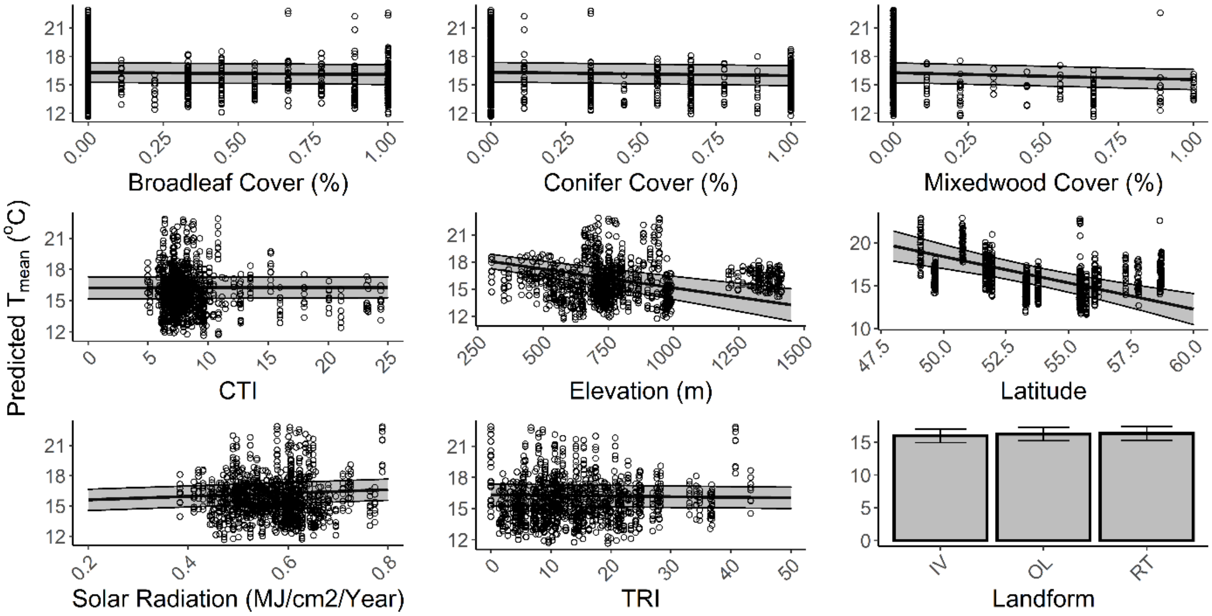


Figure 1.4: Predicted effects of topographic and vegetation variables (non-standardized) sampled on summer T_{mean} for July 2018 in hill and river valley systems in Alberta, Canada. Shaded areas around the regression line represent 95% confidence intervals. Landforms: IV – incised valleys, RT – ridge tops, OL – other landforms. See Figure S1.4 and Figure S1.5 for coefficients of other temperature metrics and other seasons.

We found that fixed effects and random effects together explained on average 40% more of the variance than fixed effects alone (conditional vs. marginal R^2; Table 1.1 and Table S1.1), indicating that site-level temperature differences were strong over the large area sampled. Conditional and marginal pseudo-R^2 values varied across seasons and temperature metrics (Table S1.1) but generally indicated that the top models of a given temperature metric explained over 60% and 35% of the variation, respectively. For the summer season, explanatory power attributed to variables was over 35% of the variation for T_{max} and T_{range} (R_m^2 = 0.36 – 0.39), over

34% for T_{mean}, and over for GDD_5 and T_{99} ($R_m^2 = 0.27 – 0.33$). For the winter season, variables explained around 35% of the variation for T_{range} ($R^2 = 0.35 – 0.39$), around 18% for T_{mean} ($R^2 = 0.16 – 0.18$), but did not perform well for T_{min} ($R^2 = 0.11$) or GDD_5 ($R^2 < 0.05$). Appendix 2 shows diagnostic plots for all metrics and models.

Mapped local climate and comparison with ClimateNA

We observed significant differences (i.e., $T_{Difference} = T_{ClimateNA}-T_{iButton}$) between ClimateNA and iButton predictions (Figure 1.5). At the station level, iButtons recorded, on average, warmer summer T_{mean}, cooler summer T_{max}, and warmer winter temperatures than ClimateNA (Figure S1.7 – S1.8). The directionality of the effect of topography and vegetation remained mostly consistent across seasons for the different metrics. Interestingly, differences in T_{max} and T_{mean} typically increased with latitude in the summer but decreased in the winter, though not always significantly.

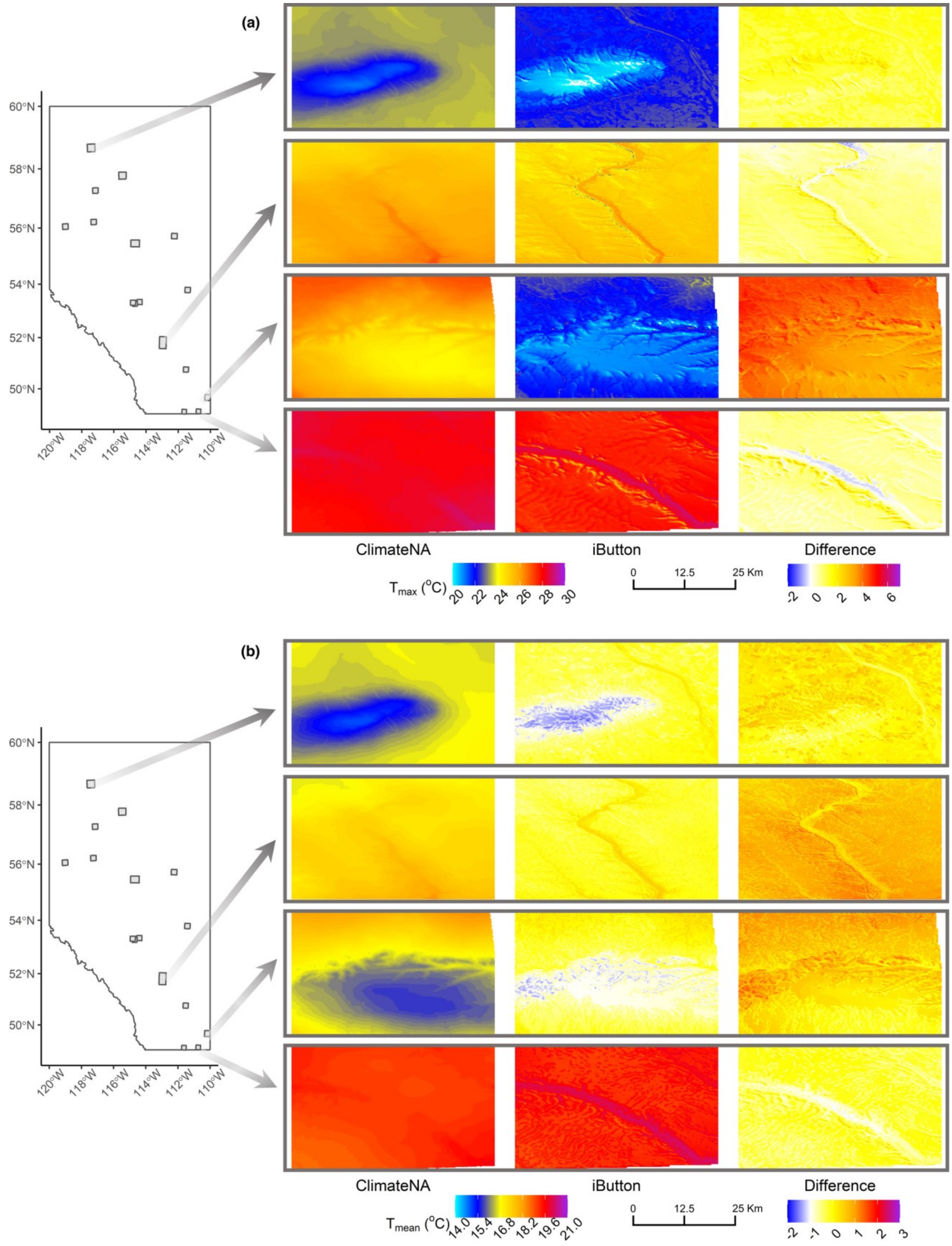

(a)
60°N
58°N
56°N
54°N
52°N
50°N
120°W
118°W
116°W
114°W
112°W
110°W
ClimateNA
iButton
Difference
T_max (°C)
20
22
24
26
28
30
0
12.5
25 Km
-2
0
2
4
6
(b)
60°N
58°N
56°N
54°N
52°N
50°N
120°W
118°W
116°W
114°W
112°W
110°W
ClimateNA
iButton
Difference
T_mean (°C)
14.0
15.4
16.8
18.2
19.6
21.0
0
12.5
25 Km
-2
-1
0
1
2
3

Figure 1.5: Spatial representation of the monthly average of summer daily (a) T_{max} and (b) T_{mean} for ClimateNA (first column) and iButtons (second column), and the difference between the two readings (i.e., $T_{Difference} = T_{ClimateNA}-T_{iButton}$; third column) over two river valley and hill systems in Alberta, Canada in July of 2018. For differences, red/blue colors indicate higher/lower temperature predictions for ClimateNA vs iButtons, while white colors indicate closer predictions between the two. For clarity, we used a specific color scheme for the differences (third column) in each panel. From top to bottom rows: Watt Mountain, North Saskatchewan River, Cypress Hills, and Milk River. Greyed squares on the left map indicate the location of all study sites.

During summer, the difference in T_{max} was ~0.22 ˚C higher on ridge tops relative to other landforms, indicating that iButtons recorded cooler T_{max} on those ridges than on other landforms. The difference in T_{max} also increased by 0.03 – 1.2 ˚C between flat and highly rugged terrain (Figure 1.6; Figure S1.7). The difference in T_{max} decreased with increasing solar radiation, indicating that iButton temperature predictions were almost 2 ˚C cooler than ClimateNA in less exposed areas and 1.3 ˚C higher in highly exposed areas when other variables were held constant at mean values (Figure S1.7). Differences in average temperature (T_{mean}) between the two sources were much smaller than differences in summer maximum. We found that the difference in summer T_{mean} in incised valleys was 0.21 ˚C higher than other landforms, indicating that iButtons recorded slightly cooler T_{mean} in these valleys than in other landforms, but still warmer than ClimateNA. Differences in T_{mean} decreased with solar radiation and indicated that iButtons and ClimateNA predicted similar values on less exposed slopes, but iButtons recorded 0.8 ˚C higher T_{mean} in highly exposed areas. We found that only coniferous forests interacted significantly with solar radiation over the summer, indicating that with low coniferous cover, iButtons recorded cooler T_{max} (~1 ˚C) in poorly exposed sites and about 1.5 ˚C warmer in highly exposed areas. The effect of solar radiation in areas with high coniferous cover was similar but not as strong, and iButtons recorded approximately 0.3 ˚C cooler T_{max} in poorly exposed sites and 1 ˚C warmer in highly exposed areas.

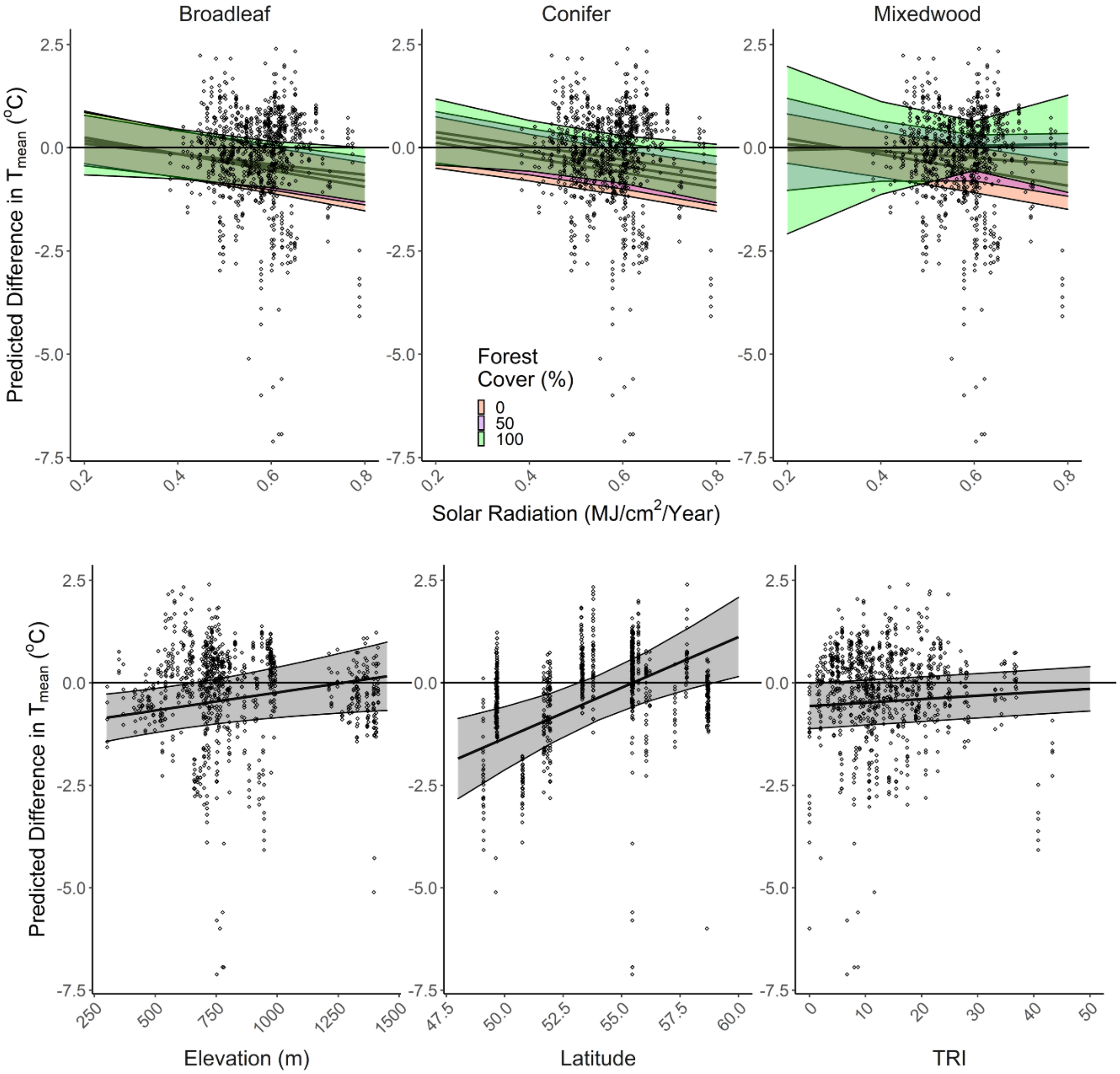


Figure 1.6: The effect of different topographic and vegetation variables on the absolute difference in summer Tmax between ClimateNA and iButton readings (i.e., TDifference = TClimateNA-TiButton). Positive values indicate that iButton measurements were higher than ClimateNA measurements. Points represent absolute differences between the two sources at the iButton station; the regression line represented the average difference with 95% confidence intervals. Horizontal black line indicates no

difference between ClimateNA and iButtons. Only significant variables at α = 0.05 are presented.

We found that for winter T_{min}, iButtons predicted warmer temperatures than ClimateNA (Figure S1.8). The difference in T_{min} in incised valleys was 0.39 ˚C higher relative to other landforms, indicating that iButtons recorded cooler T_{min} in incised valleys than in other landforms. ClimateNA predictions were -3.28 ˚C to -1.90 ˚C lower than iButtons in areas with low and high topographic wetness potential, respectively. Furthermore, we found that an interaction between broadleaf forests and solar radiation led to smaller differences in winter T_{min} in areas with low broadleaf forest cover and poorly exposed, where ClimateNA predicted on average 1.8 ˚C cooler temperatures than iButtons. Differences in T_{min} also got smaller in areas with higher broadleaf forest cover and high exposure, and ClimateNA predicted temperatures that were 2.5 ˚C cooler than iButtons. Across metrics, elevation had mostly no significant effects on the difference between the two sources (Figure S1.7 – S1.8), except that iButtons significantly recorded ~0.86 ˚C warmer T_{mean} in low elevations and ~0.12 ˚C cooler T_{mean} in high elevations (Figure 1.6). Differences in winter T_{mean} were consistent as iButtons recorded warmer temperatures with increasing elevation (up to ~3.75 ˚C; Figure S1.8).

iButton predictions had a higher level of spatial heterogeneity than ClimateNA, linked to the effects of topographic variables (see Figure 1.5 for an illustration). Differences in summer maximum temperatures were larger in the drier and hotter hills in the southeastern part of Alberta (Cypress Hills; Figure 1.5, third row).

Discussion

In this study of a 1000+ km span of the boreal-parkland-grassland transition zone in western Canada, we found compelling evidence that despite gentle to moderate amounts of terrain (hill and valley systems), local topography and vegetation still have significant buffering effects on local climates. We found that not only did elevation drive differences in local climates, but roughness, aspect, landform and vegetation also exerted significant effects. More specifically, topographically shaded sites were between 0.7 – 2.9 ˚C cooler than flat, exposed sites in both summer and winter, while sites with more surrounding forest cover were up to 0.7 ˚C cooler in summer and 2 ˚C warmer in winter than non-forested sites. By extension, we demonstrated that local topographic effects on temperature are not fully captured in commonly used downscaled gridded climate data products.

Effects of topographic factors and vegetation on local climate

Elevation – Elevation was one of the strongest single predictors for most temperature metrics. We found that elevation decreased mean summer temperatures by almost 6 ˚C over the 1400 m elevation gradient that we evaluated and increased minimum winter temperatures by up to 5.5 ˚C, indicating winter temperature inversions. However, we found more support for models relating temperature metrics to a combination of local topography and vegetation cover. Models that accounted only for elevation received relatively little support and, in general, had lower explanatory power relative to full models. Hence, our results demonstrate that a combination of topographic factors is needed to explain local temperature variations, and therefore local heterogeneity. Landscapes with more gentle terrain, such as the prairie-parkland-boreal plain transition in Alberta, are projected to exhibit high climate change velocity compared with mountainous regions (Carroll *et al.*, 2015; Brito-Morales *et al.*, 2018). However, we found that the existing topography in these transition zones creates substantial thermal heterogeneity not captured by gridded climate data products.

Solar radiation – Not surprisingly, we found an important influence of aspect and slope, via differences in solar radiation, with highly exposed slopes being up to 2.9 ˚C warmer than shaded areas for summer T_{max}. However, the effect was smaller than what has been found in mountain systems (Geiger, Aron and Todhunter, 1995; Gruber, Hoelzle and Haeberli, 2004; Huang *et al.*, 2008; Suggitt *et al.*, 2011). For instance, differences of 6 ˚C in mean annual temperature between the north and south-facing slopes have been observed in steep mountainous terrain (e.g., Swiss Alps, Gruber, Hoelzle and Haeberli, 2004), while smaller mountains (~300 m elevation gradients) have shown differences of 7 ˚C in maximum temperatures and 1.3 ˚C in mean temperatures (Wales and England, Suggitt *et al.*, 2011). These differences are much greater than what we found and may be related to the shape of the topography we sampled, which can influence wind turbulence and the dynamics of cold and warm air. Relatedly, differences in climate conditions, steepness of elevational gradients and instrumentation can also lead to steeper temperature gradients (Geiger, Aron and Todhunter, 1995). Perhaps most importantly, the angle of a slope influences the solar radiation difference between aspects and probably explains much of the difference between results found here and those from studies in more rugged terrain. Finally, these differences could also be related to differences in radiation shielding (Maclean *et al.*, 2021; Terando *et al.*, 2017) and the efficacy of our shielding vs. simpler approaches (see Suggitt *et al.*, 2011 for more details).

Topographic wetness – We did not find an effect of topographic wetness on maximum temperatures for the summer period, but we found evidence that it decreased winter minimum and mean temperatures. The compound topographic index (CTI) is a proxy for among other things soil water accumulation associated with topography (Gessler *et al.*, 1995; MacMillan *et al.*, 2000). In moisture-limited systems, such as ours, decreased soil moisture should lead to increased summer temperatures via reduced evapotranspiration (Seneviratne *et al.*, 2010; Schwingshackl, Hirschi, and Seneviratne, 2017). The fact that we did not observe this effect may be due to the digital elevation model (DEM) proxy used, which does not consider soil texture or other aspects of water storage capacity. Furthermore, CTI is scale-dependent and DEM resolution influences the catchment area upstream and leads to more irregular flow pathways, which ultimately affects calculated indices (Sørensen *et al.*, 2007). The negative relationship with winter temperatures that we found suggests the potential for cold-air pooling in low-lying areas. However, it is important to note that CTI is a relative metric, in the sense that ravines at higher elevations can still have high CTI and likewise lower elevation areas can have low CTI.

Terrain roughness – We found some evidence that local terrain variability may affect temperatures at local scales, because the topographic roughness index (TRI) decreased summer T_{max}, T_{mean}, and T_{range}. Roughness increases air motion and leads to greater vertical and horizontal mixing of air due to differential heat of slopes locally, which in turn can reduce temperature extremes (high and low) near the surface (Gloyne, 1967). Our results suggest that air mixing may be reducing both maximum and minimum extremes and that even the limited amounts of terrain roughness found in river valleys and boreal hills can partially buffer extremes in temperature. However, it is important to note that the effects of terrain roughness can be quite localized, particularly considering wind dynamics in complex topography (e.g., Helbig *et al.*, 2016). Consequently, iButtons could be experiencing high degrees of variation in local temperature due to differential winds, even though we detected lower temperatures on average (Wood and Mason, 1993).

Landform – Relative to other landforms, temperature was generally lower in incised valleys during the summer, but we did not observe lower winter minimum temperatures in valley bottoms, relative to other landforms. We did find a positive effect of elevation on minimum temperature in the winter, suggesting that winter temperature inversions are common in larger valleys. However, our landform categories considered a variation of neighboring cells at a small scale (300-m radius around each pixel). Therefore, “valleys” and “ridgetops” represent small ravines and coulees that are less prone to temperature inversions. Rather they are likely associated with topographic shading, leading to negative effects on local temperatures overall.

Vegetation cover – Our results examining the effect of vegetation cover partially supported previous studies, in that surrounding forest cover led to decreased mean temperatures in summer and increased minimum temperatures in winter (e.g., De Frenne *et al.*, 2021). Consistent with other studies from boreal forests (as summarized by De Frenne *et al.*, 2021), we found a stronger positive buffering effect on winter minimum temperatures compared to summer mean temperatures. This could be at least partly explained by the type of shielding we used for our iButtons, which is very effective at blocking direct solar radiation and can be slightly biased towards cooler temperatures in forested environments relative to commercially available shielding (Holden *et al.*, 2013). Interestingly, we found that broadleaf vegetation cover had positive effects on summer temperature maxima. This could be the result of the moisture-limited conditions that characterize the boreal-parkland-grassland transition zone (e.g., Koster *et al.*, 2004; Seneviratne *et al.*, 2010) because the cooling effects by evapotranspiration decrease under moisture-limited conditions (Davis *et al.*, 2019). Deciduous-dominated areas may be drier than coniferous vegetation, which may reflect in warmer temperatures (Martin-Guay *et al.*, 2022). In addition, forest cover in the prairie and parkland portions of our study area is closely associated with north-facing slopes, which we found to be an important negative predictor of maximum temperature (via the solar radiation metric we used), so the effect may be captured within that variable.

Canopy structure, including height and tree age, as well as moisture, have been proposed as important factors promoting the cooling of local climates (Renaud and Rebetez, 2009; von Arx, Dobbertin and Rebetez, 2012; Milling *et al.*, 2018; De Frenne *et al.*, 2021). Moreover, the canopy energy balance in boreal forests displays different patterns depending on forest composition. Coniferous forest canopies have higher aerodynamic roughness relative to deciduous dominated forests, which could lead to a decrease in air temperature locally (McCaughey *et al.*, 1997; Blanken *et al.*, 2001). Although we did not measure local canopy cover, this agrees with our results that increasing levels of surrounding coniferous and mixedwood forest had a negative effect on summer T_{mean}. In addition, forested plots can retain heat within the understory by blocking outgoing longwave radiation at night, thereby exhibiting higher minimum temperatures relative to treeless areas (Davis *et al.*, 2019; De Frenne *et al.*, 2021). Although we found that surrounding forest cover buffered minimum annual temperatures (i.e., winter T_{min}), we did not find a diurnal buffering of minimum temperature in summer, suggesting that other factors like topographic shading may have been overriding.

Mapped local climate and comparison with ClimateNA

Compared to a downscaled gridded climate product (ClimateNA), our estimates showed a similar regional pattern of air temperature but highlighted the thermal heterogeneity of the landscape. Elevation had mostly no noticeable influence on the difference between the two sources of data in summer, which suggests that they are capturing similar lapse rates and regional patterns in warm months. However, iButton data indicated a larger reduction in winter minimum and average temperatures at higher elevations, suggesting winter temperature inversions that are not captured in ClimateNA (e.g., Figure S1.10 – S1.11). Locally, the magnitude of the difference between the two estimates was greatest in areas where iButton data predicted warmer temperatures (i.e., exposed and/or non-forested slopes), but smaller where our estimates predicted cooler temperatures (i.e., areas with high topographic shading). Since local climates are a result of the effects of local ecosystem functioning and landscape properties that modify the climate at larger scales (mesoclimate; Geiger, Aron and Todhunter, 1995; Chen *et al.*, 1999; Bailey, 2009), gridded climate products don't capture the resulting thermal nuances in the landscape.

We also observed a substantial effect of latitude on the difference between ClimateNA and iButton measurements (generally positive in summer and negative in winter). Such differences may be related to the negative relationship between elevation and latitude in Alberta. Another possibility is the fact that we centered our solar radiation potential variable at a single latitude (see Methods section) and solar radiation decreases with latitude, which could be driving the difference with our northern sites. Of course, estimates from either source of data may have inherent biases derived from different instrumentation (weather stations vs. local climate sensors; Ashcroft, 2018). For instance, differences in T_{mean} between the two products were smaller than differences in T_{min} and T_{max}, suggesting either that iButtons are more susceptible to temperature extremes (Maclean *et al.*, 2021) or that ClimateNA overestimates them. iButton warm biases could be considerable in open environments if heat shields are not properly equipped (Maclean *et al.*, 2021), although we do not believe that was an issue in our study, given the effectiveness of the Holden *et al.* (2013) shield design. Acknowledging these limitations, it is clear that interpolated climate products such as ClimateNA cannot fully describe the thermal heterogeneity that has implications for climate-change adaptation at local and regional scales (e.g., Greenwood *et al.*, 2016).

Implications for climate-change adaptation

Overall, we found evidence that the combined effects of local topography and vegetation exerted a substantial influence on local temperatures. Also, their impact was comparable in magnitude to the cooling effect of elevation, even in the moderate topography of the boreal-parkland-prairie transition zone. Notably, some of the topographic and vegetation effects analyzed may promote a level of cooling that falls within near-term climate change projections for this region. We found that areas with a low incidence of solar radiation, such as north-facing slopes and incised ravines, may have maximum temperatures that are up to 0.7 ˚C and 2.9 ˚C cooler than surrounding areas during summer, while terrain roughness may further contribute 1.62 ˚C. Furthermore, we found that sites with greater levels of surrounding coniferous and mixed forest cover can experience local mean summer temperatures that are nearly 1 ˚C cooler than open sites, supporting the notion that the inherent local buffering capacity of forests might be on the same order of magnitude as expected future warming (Frey *et al.*, 2016). Combined, the buffering capacity of topographic and vegetation effects may be comparable to the expected ~2 ˚C increase by 2050 and ~3 ˚C by 2100 in the boreal plains (Price *et al.*, 2013). Boreal species that can shift to or persist in these cooler areas might be able to compensate for regional warming.

A contemporary example of this cooling effect is the presence of coniferous forest patches on north-facing slopes in central Alberta, at the limit of drought tolerance for boreal trees. These patches are relict populations of boreal forests that once occupied the southern part of the region (e.g., Hampe and Jump, 2011). Thus, they may be analogs for how the current boreal forests in the north may be distributed in the future under climate change. In other words, the norm across northern Alberta could become patches of coniferous and mixed forest, mainly on north-facing slopes and other sheltered sites, interspersed with grassland and open parkland. Conversely, south-facing slopes, and areas with low surrounding forest cover are more susceptible to warming and rapid climate change at the local scale. Our results suggest that the combination of forest cover and topographic setting has the potential to buffer the effects of near-term climate change, although the level of future persistence is uncertain (Lembrechts and Nijs, 2020; Zellweger *et al.*, 2020; De Frenne *et al.*, 2021; De Lombaerde *et al.*, 2022).

Our results provide empirical support for topographically- and vegetation-mediated temperature variation that may result in refugia for forest-associated species under a warming climate (Stralberg *et al.*, 2020). Understory-dwelling plants and animals could benefit directly from canopy shading, while birds and other wildlife can benefit from forest patches retained by cooler conditions, which could be used as stepping stones as their climate niches shift northward with continued climate change. With the adoption of conservation measures and targeted forest management practices, topographically sheltered forest stands may serve as "slow-lanes" that buffer the negative effects of climate change in the short term and provide safe havens in the long term (Morelli *et al.*, 2020). Such practices could include the implementation of riparian buffers, strategic retention patches, and afforestation (Greenwood *et al.*, 2016). Conservation and management strategies that target refugia and the landscape features that promote them can serve as efficient investments for short- and long-term conservation goals in a changing climate.

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Data Accessibility Statement and supplementary information

Data used for this research is available through Dryad under the title "*Topographic and vegetation drivers of thermal heterogeneity along the boreal–grassland transition zone in western Canada: implications for climate change refugia*", https://doi.org/10.5061/dryad.f7m0cfxw2.

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Chapter 3 – Climate downscaling reveals important interactions between habitat and climate for boreal songbirds

Summary

Identifying areas relatively resilient from climate-change, or refugia, is a potential adaptation strategy for biodiversity conservation. For forest-associated wildlife, refugia may be related to climate at different scales. We sought to quantify climate-change refugia for forest songbirds in Alberta, Canada and explored differences between macroclimate (unadjusted) and locally adjusted climate predictions of refugia. We surveyed songbirds with autonomous recording units (N=2147 locations) from spring to mid-summer between 2014 – 2018 and monitored local climate with iButton dataloggers (N=283) in river valleys and hills systems in Alberta, Canada. We modeled the difference between iButtons and macroclimate predictions as a function of a suite of derived topographic variables and tree cover to generate climate offsets to downscale macroclimate. We then modelled the occurrence of 48 songbird species as a function of the relative biomass of boreal tree species, habitat variables and climate (adjusted and unadjusted) using generalized boosted regression trees. For each species we fit four models representing all combinations of (i) adjusted vs. unadjusted climate and (ii) climate-only vs. climate + vegetation variables (full model). We classified bird species based on their nesting preferences (coniferous-, wetland- or deciduous-associated species) and evaluated the average change in relative importance of variables and change in explanatory power (pseudo-R^2) after adjusting climate. We then predicted refugia potential as the area of overlap between current and future distribution under a moderate climate scenario. We observed that the explanatory power of models improved using adjusted vs unadjusted climate conditions for 19 and 15 out of 48 species for the full and climate-only models, respectively, suggesting that most species may not be as sensitive to local climate. The relative influence of environmental variables decreased for most groups after using adjusted climate variables. However, climate variables increased in influence for coniferous-associated species, suggesting that this group may be more sensitive to climate at small scales. Our models predicted more refugia area for coniferous-associated species than any other group. Loss of current suitable habitat was smallest for coniferous-associated species when using adjusted climate in the climate-only model (21% vs 58% with unadjusted variables), but the opposite was true for the full model (39% vs 23% with unadjusted variables). For deciduous-associated species, loss of suitable habitat was smaller when using adjusted climate regardless of model used, which could be related to projected increases in occurrence for this group with climate change. The refugia centroid for coniferous-associated

species with adjusted variables predicted a smaller northward change than unadjusted variables for the full model, relative to centroid of their current habitat suitability. Overall, our results suggest that coniferous-associated species may be more sensitive to local climate conditions than the other groups, which seem to be driven by climate at a regional (or macro) scale. Areas with high refugia potential in the study area could be used by managers to target conservation efforts for coniferous-associated species.

Introduction

Climate change impacts on ecosystems and consequences to human welfare are an increasing concern. The Intergovernmental Panel on Climate Change (IPCC) has emphasized that substantial efforts are needed to reduce extensive losses in biodiversity caused by climate change. Increasing temperatures will not only stress the physiology of organisms, but will also lead to mostly northward shifts in species ranges in the northern hemisphere (Virkkala and Rajasärkkä, 2011). Habitat degradation and loss because of climate change are expected to reshuffle ecological communities and ecosystems in a short timeframe for several wildlife species (Stralberg *et al.*, 2009; Price *et al.* 2013; Schneider, 2013). This scenario has led to growing efforts to mitigate the effects of climate change by establishing policies to reduce our reliance on fossil fuels, therefore reducing greenhouse gas emissions. However, the timespan for these strategies may not be fast enough to allow for species to adapt to the novel and unsuitable conditions that are already developing. For conservation to be effective we need to establish adaptation strategies that give us the greatest chance of conserving biodiversity until climate stability has been reached.

Identifying climate-change refugia is a potential adaptation strategy for biodiversity conservation. Climate-change refugia have been defined as “areas relatively buffered from contemporary climate change over time…” (Morelli *et al.*, 2016). Such areas may warrant greater protection from other sources of human-induced change (e.g., land-use change, increased wildfire activity). To identify refugia, it is important to define what we are defining refugia for, where refugia are likely to be, and how long they will potentially last (Stralberg et al. 2020). Refugia can be defined for entire ecosystems or for individual species (Carroll et al. 2015). Where refugia are located now and in the future relies on understanding species niches and habitat requirements. For forest-associated wildlife, climate-change refugia will be related to the composition, structure, and other attributes of the forests the species inhabit, but also the role that vegetation cover plays in regulating climate at the local scale (De Frenne *et al.*, 2021), and the cumulative topoedaphic processes that regulate climate at different spatial scales

(Estevo *et al.*, 2022). For example, north-facing slopes in valleys along the grassland-boreal transition biome in western Canada create cooler conditions due to topographic shading, which allows patches of moisture-sensitive conifers to grow, further enhancing a cooler local climate, despite the dry regional conditions that are inhospitable to tree growth (Estevo *et al.*, 2022). However, the value of these small, isolated forest patches as refugia for boreal wildlife (e.g., songbirds) remains unclear.

Traditionally, broad-scale bioclimatic models have been used to identify changes in species distribution due to climate change (e.g., Elith *et al.*, 2006; e.g., Lawler *et al.*, 2009; Araújo and Peterson, 2012; Stralberg *et al.*, 2015). Bioclimatic models provide a baseline to evaluate potential changes in the future distribution of wildlife. In refugia studies, species distribution models (SDM) have been used to identify refugia based on the overlap of current and future projected species range (Stralberg et al. 2015, Bateman et al., others). Models are typically based on coarse resolution (typically 1-10 km) “macroclimate” data and ignore topoedaphic and vegetation impacts on microclimate. Potential shortcomings of macroclimate models include lower explanatory power (Slavich *et al.*, 2014), overestimation of species’ thermal tolerances (Trivedi *et al.*, 2008), and in some cases underestimation of species persistence (Randin *et al.*, 2009).

Downscaling of macroclimate may be essential in overcoming some of these shortfalls. Downscaling consists of increasing the resolution (or decreasing the grain size) of climate grids through various techniques. *In-situ* measurements of temperature may allow users to interpolate measurements (Ashcroft, Chisholm and French, 2008; Slavich *et al.*, 2014), but this approach has limited ability to cover broad spatial extents. Another approach is to combine *in-situ* measurements along with habitat features to develop descriptive distribution models of local climate (Frey, Hadley and Betts, 2016). In cases where *in-situ* measurements are not available, topographic variables derived from digital elevation models (DEM; e.g., slope aspect, terrain roughness) have been use as proxies for microclimate variables and included directly into SDMs (Patsiou *et al.*, 2014, Oke et al. 2022). Although at high spatial resolution these variables are powerful proxies for microclimatic differences in habitat in the current period, such variables are static and not projected forward with climate change. Conversely, statistical downscaling correlates *in-situ* climate measurements (e.g., subcanopy temperature) with remotely sensed information or other DEM-derived topoclimatic metrics (Lembrechts, Nijs and Lenoir, 2019). These can then be used to develop temperature offsets, which are then combined with climate grids available at larger scales to incorporate small-scale forcing factors (e.g., Holden *et al.*, 2016). We refer to this approach as *climate adjustment*. Aligning these small-scale processes increases the resolution at which suitable habitat may be predicted. However, the extent to which climate adjustment increases windows of opportunity for conservation remains uncertain, as downscaling may result in more or less climate-predicted loss depending on each species (Davis *et al.*, 2016; Lenoir, Hattab and Pierre, 2017). Thus, the comparison of results based on climate adjustment may improve our understanding of species' differential responses to climate change. Despite this potential, the incorporation of local climates into species distribution models over large extents is still in its infancy. Most studies in this realm have focused on sessile organisms (e.g., Slavich *et al.*, 2014), with limited examples on mobile organisms (e.g., songbirds, Frey *et al.* 2016).

We maintain that downscaling climate models to identify small-scale refugia may be an essential element of conservation planning because further conservation opportunities may arise once small-scale processes are accounted for. Therefore, we sought to quantify climate-change refugia for passerine bird species (hereafter songbirds) in the boreal forest of Alberta, Canada and to compare the roles of macroclimate and local climate in understanding the distribution of species. More specifically, our objectives were to (1) understand the impact that climate adjusted variables have on the relative importance of vegetation and climatic factors on species distribution, (2) quantify the impact that climate adjustment may have on the performance of species distribution models and the future distributions of songbird groups, and (3) compare and quantify refugia potential based on climate information at different scales (i.e., macroclimatic (unadjusted) vs. climate-adjusted models). We did this by building temperature offsets based on topographic downscaling (Estevo et al. 2022), while using equivalent grain size and extent across climate variables. We hypothesized that incorporating small-scale climate conditions into refugia identification would lead to more high-potential refugia areas being identified for the different songbirds but that their distribution would be patchier as local climate is more thermally diverse than what is estimated using macroclimate only. We also had specific expectations for the different groups of birds analyzed. We expected coniferous-associated bird species to gain more refugia after incorporating adjusted climate variables, as coniferous forests in this region (primarily dominated by white spruce, *Picea glauca*), are associated with cooler climates (threatened by climate change), and topographic downscaling should capture small areas suitable for coniferous-associated species, particularly within the boreal-grassland transition zone (Estevo *et al.*, 2022). Meanwhile, we anticipated that deciduous-associated bird species may not exhibit as much difference given that deciduous forests (primarily dominated by aspen, *Populus tremuloides*) may replace spruce in boreal regions as the climate warms (Hogg and Hurdle, 1995). We expected that wetland-associated species would not see much difference in refugia potential after adjusting climate because wetlands mostly occur in flat, low-lying regions of the boreal biome (Moss, 1955; Schneider *et al.*, 2009), with little potential for topographic buffering of temperatures.

Methods

Study area

Our study area encompassed the entirety of the grassland-boreal zones in the western province of Alberta, Canada (Figure 2.1). Alberta contains a latitudinal gradient from grasslands and open environments in the far south, which are characterized by a hot and dry season over the summer, and boreal forests in the north, where temperatures are milder and conditions tend to be wetter than in the grasslands primarily due to greater snowfall. The parkland region in mid latitudes consists of a transition zone between boreal and grassland environments, with a mix of deciduous and coniferous tree species interspaced by grassland mosaic. The transition grassland-parkland-boreal forest is tightly regulated by a precipitation and evapotranspiration regime that directly affect the distribution of the major tree coniferous species in the boreal biome at their southern limit. The main coniferous species include white and black spruce (*P. mariana*, respectively). Deciduous trees consist mostly of trembling aspen, a widespread tree in North America, birch (*Betula papyrifera*) and cottonwood (*Populus deltoides*). Cypress Hills, in the far southeast corner of the province, is a high elevation area that remained unglaciated during the advancement of Laurentian icesheet that contained relict vegetation. It now hosts white spruce, lodgepole pine (*Pinus contorta*), and aspen forests.

Topography is limited in most of Alberta except in the Rocky Mountains and the foothills. Most of the province is dominated by gentle terrain, and roughness occur in major river valleys, and hill systems created by differential fluvial erosion of sedimentary bedrock. At large scales, the limited relief is described as one of the main reasons why species might have to migrate faster over the landscape to maintain constant climatic condition (i.e., climate velocity, Loarie *et al.*, 2009; Hamann *et al.*, 2015). However, the presence of white spruce currently in north-facing slopes across all of Alberta suggest that local climate variability and heterogeneity has historically buffered the unfavorable dry and hot conditions for boreal trees in the flatter portions of the province (Estevo et al. 2022) suggesting that climate velocity may not be as high if climate data are topographically downscaled.

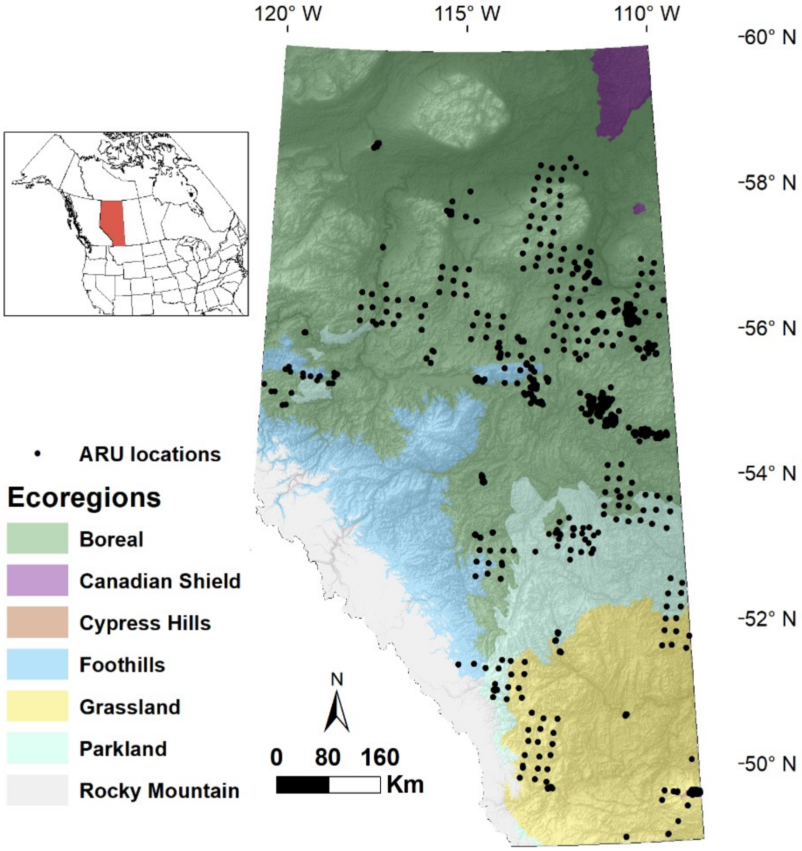


Figure 2.1: Location of autonomous recording units (ARUs) to detect songbirds within the different ecoregions in Alberta, Canada.

Bird occurrence data and environmental variables

Following similar steps from Estevo (2022), we used data collected by the Bioacoustic Unit and the Alberta Biodiversity Monitoring Institute and available via WildTrax (https://wildtrax.ca). We used acoustic detections of songbirds surveyed with autonomous recording units (ARU; Shonfield and Bayne, 2017) in 2147 locations that were set up with a pre-defined schedule from sunrise to mid-morning in spring and mid-summer (May 15 to July) between 2014 – 2018. We then identified birds by sound and assigned presence (1) or absence (0) of each species for each site and day of recording to build an encounter history for occupancy modelling. We tried to sample birds for four days at each ARU, but sampling varied across different sites (from 1 to 4 days) due to adverse weather conditions. We classified all forest associated songbird species detected with ARUs (N=48 species) into three groups based on their nesting habitat association: coniferous-, deciduous-, and wetland-associated species. The list of species included species whose >50% of their population breed in the boreal biome, based on information from the Boreal Songbird Initiative website (https://www.borealbirds.org/), as well as other species currently present in the boreal but not restricted to it. Our goal was to include species that are strongly associated with the boreal biome, and that are more likely to face the biggest effects of climate change in the region, as well as birds on the other end of the spectrum, that could in fact benefit from a warming climate.

We used a suite of environmental variables to model avian species distribution (Table 2.1). For vegetation and habitat structure, we extracted the relative biomass of trees estimated using the Canada's National Forest Inventory combined with MODIS satellite imagery (Beaudoin *et al.*, 2018). More specifically, we extracted the estimated biomass of conifers (white and black spruce), birch (Betula spp.), and 'poplars' (aspens and poplar, Populus spp.), crown closure, and age of the leading species.

Because vegetation biomass data are at coarse resolution and subject to classification error, we also used a more direct index of vegetation productivity. For that, we calculated the normalized differential vegetation index (NDVI) for the boreal summer period (June, July, and August) from 2012 – 2018 as a proxy of overall forest greenness and productivity based on the time series of images from Sentinel-2 collected by the European Space Agency. Using Google Earth Engine, we filtered the image collection for pixels that contained <30% of granule-specific clouds taken from the original metadata, made composite maps for each year using the median of each pixel and calculated NDVI for that year. We then averaged the six-year periods of NDVI to generate a single NDVI image for Alberta. We also calculated an index for patch area where we deployed each ARU. To do that, we defined forests by rasterizing the different forest categories (coniferous, broadleaf and mixed forests) from the wall-to-wall mapping tool developed for Alberta (Alberta Biodiversity Monitoring Institute, ABMI, Version 2.1, circa 2010) and generated a single raster of presence-absence of forest at 50 m resolution. The wall-to-wall map was created based on digital classification of 30 m of spatial-resolution Landsat satellite imagery. Then, we used *windows_lsm* function within *landscapemetrics* package (Hesselbarth *et al.*, 2019) in R environment (R Core Team, 2013) to identify individual patches of forest within a moving window of 21 x 21 pixels (approx. 2 x 2 km) following up by calculating the average patch area for a focal cell within that neighborhood. We extracted wetland probability for each ARU station from the Boreal Wetland probability dataset developed by ABMI (Hird *et al.*, 2017).

We used the application ClimateNA version 7.30 (Wang *et al.*, 2016 and details within) to generate normal and future macroclimate (hereafter, unadjusted) climate projections for Alberta. Using a digital elevation model (DEM) at 250 m, we generated spatially explicit estimates of summer climate moisture index (CMI), summer precipitation (summer precip), growing degree days (GDD>5), and mean minimum winter temperature (Tmin). For current periods, we extracted variables for the 1961 – 1990 normal period, as well as projected temperatures for the end of the century (2070 – 2100) based on a moderate ensemble of GCMs driven by Shared Socioeconomic Pathways scenario (SSP 370) (IPCC, 2007).

To develop the adjusted climate projections, we used the approach developed by Estevo *et al.* (2022), where data from iButton dataloggers were deployed in river valleys and hills systems (N=283) in Alberta to generate offsets of CMI and Tmin by using a modified approach from Holden et al. (2016). To do this, we first calculated the difference between iButtons and ClimateNA predictions at each iButton location for the same years the iButtons were deployed and then modelled the difference as a function of a suite of topographic derived variables and tree cover (Estevo *et al.*, 2022). We then created spatial predictions of these offsets and added them to their corresponding variable for the normal and future periods to generate adjusted climate variables that represent local climates (Figure 2.2). We excluded the Rocky Mountains ecoregion, where climate variability is high as a function of terrain variability, because of lack of data.

All spatial layers were resampled from their native resolution to a 250-m resolution with a nearest neighbor setting.

Table 2.1: Abbreviation and definitions of environmental variables used in the modelling.

Category	Variable	Units	Definition
Vegetation	Poplars	%	Relative biomass of poplars (Populus spp.)
	Birch	%	Relative biomass of birch (Betula spp.)
	Wspruce	%	Relative biomass of white spruce (*Picea glauca*)
	Bspruce	%	Relative biomass of black spruce (*P. mariana*)
Climate	DD5	-	Growing Degree Days
	MSP	mm	May to September precipitation
	CMI	-	Summer climate moisture index

	Tmin	mm	Mean Minimum Winter Temperature
Habitat	Age	years	Age of leading species
	NDVI	-	Normalized difference vegetation index
	PAr	ha	Average patch area within a 21 x 21 window
	Wetprob	%	Wetland probability
	Cclosure	%	Crown closure

Bird species distribution models and relative influence of environmental variables

We built occupancy models (Mackenzie et al., 2005) for each species, with a null model (*Ψ(.)*) for occupancy and time of the acoustic recording, Julian date and the amount of forest (%) in a 200 m radius around each ARU as a predictor of detection probability (*p*). We derived the amount of forest based on the wall-to-wall mapping tool from the Alberta Biodiversity Monitoring Institute by merging presence-absence rasters of coniferous, broadleaf and mixedwood forests and then calculating forest cover in a 300-m radius buffer around each ARU station. We chose to use the wall-to-wall product because it was derived directly from Landsat imagery, and likely yields a more precise representation of forest cover, relative to the national forest inventory-based product (Beaudoin et al. 2014), which is coarser but species-specific. All ARU stations had <50% human disturbance (including agriculture) within a 300-m buffer. After building occupancy models, we extracted the conditional probabilities of occurrence based on the suite of detection variables. We did all occupancy modelling in R (R Core Team, 2013) with the *unmarked* package (Fiske and Chandler, 2011).

Our next step was to fit conditional occupancy probabilities using generalized boosted regression trees (BRT) fit with the *gbm* package (Greenwell *et al.*, 2022) in R. BRTs have the advantage that the model structure is learned from the data, which avoids assumptions required in model specification. It can fit multiple nonlinear relationships, automatically handles predictor interactions, and better accommodates the patchiness of species distribution in vast environmental spaces (Elith, Leathwick and Hastie, 2008). We build models where the conditional occupancy of each songbird was a function of the relative abundance of tree species (white spruce, black spruce, birch, poplars), mean tree age, crown closure, patch area index, wetland probability, NDVI, and climate. We developed two sets of *full models* and two sets of *climate-only* models for each species. Full models contained (i) all environmental variables plus unadjusted macroclimate and (ii) all variables plus topographically downscaled (adjusted) climate. Climate-only models were based on (i) unadjusted macroclimate and (ii) adjusted climate. For each species we trained models with 80% of the data and used the remaining 20% to test models and calculated pseudo-R^2 for each model. As a final step, for each model we extracted the relative importance of each variable and weighted each relative impact by multiplying it with the pseudo-R^2 for that model. Weighted importance values for each variable were then averaged across species within each nesting group.

For future projections, we chose to keep vegetation and other habitat features static over time and focus our analysis on the climatic effects of future songbird distribution and refugia potential. Although this is somewhat unrealistic, we bookended our projections by comparing with climate-only versions of the models, representing a scenario in which vegetation perfectly tracks changes in climate. The situation is likely to be intermediate to these extremes, but it was outside of the scope of this paper to model the influence of disturbance and succession on vegetation change.

Spatial predictions, refugia potential area and location

To develop refugia potential maps, we first created current and future (2071-2100) spatial predictions of the models described in the previous section. We used a moderate warming scenario for all future predictions of songbirds (SSP 370). We then reclassified both current and future predictions rasters to a binary form (presence/absence), using the mean probability of occurrence within the study area during current period as a threshold for occurrence. That is, if the probability of occurrence at a given pixel was greater than this prevalence threshold, we assigned a value of 1, and a 0 value was otherwise assigned (Manel, Williams and Ormerod, 2001). We repeated this process per model, such that the prevalence threshold varied by model prediction. Visual inspection confirmed that the prevalence maps aligned with species ranges. We then added both the current and future rasters together and classified the pixels with overlap as areas of potential refugia. By following this procedure, our final result consisted of refugia maps per species. We followed up by summing the number of pixels with refugia for each species (per model) to calculate the total amount of refugia area per species. We then calculated the percent difference in area between the current area of occurrence and refugia predictions per model and songbird group. Finally, we generated overall refugia potential maps per songbird group by adding all the species refugia rasters of each songbird group together. We normalized each species group to create refugia index maps that ranged from zero (no overlap between current and future distribution for any species in a pixel) to one (maximum overlap per pixel for that species group). We then calculated the difference between climate-only and full (climate + vegetation) model refugia predictions (adjusted minus unadjusted maps) to highlight differences between predictions that used adjusted or unadjusted climate variables.

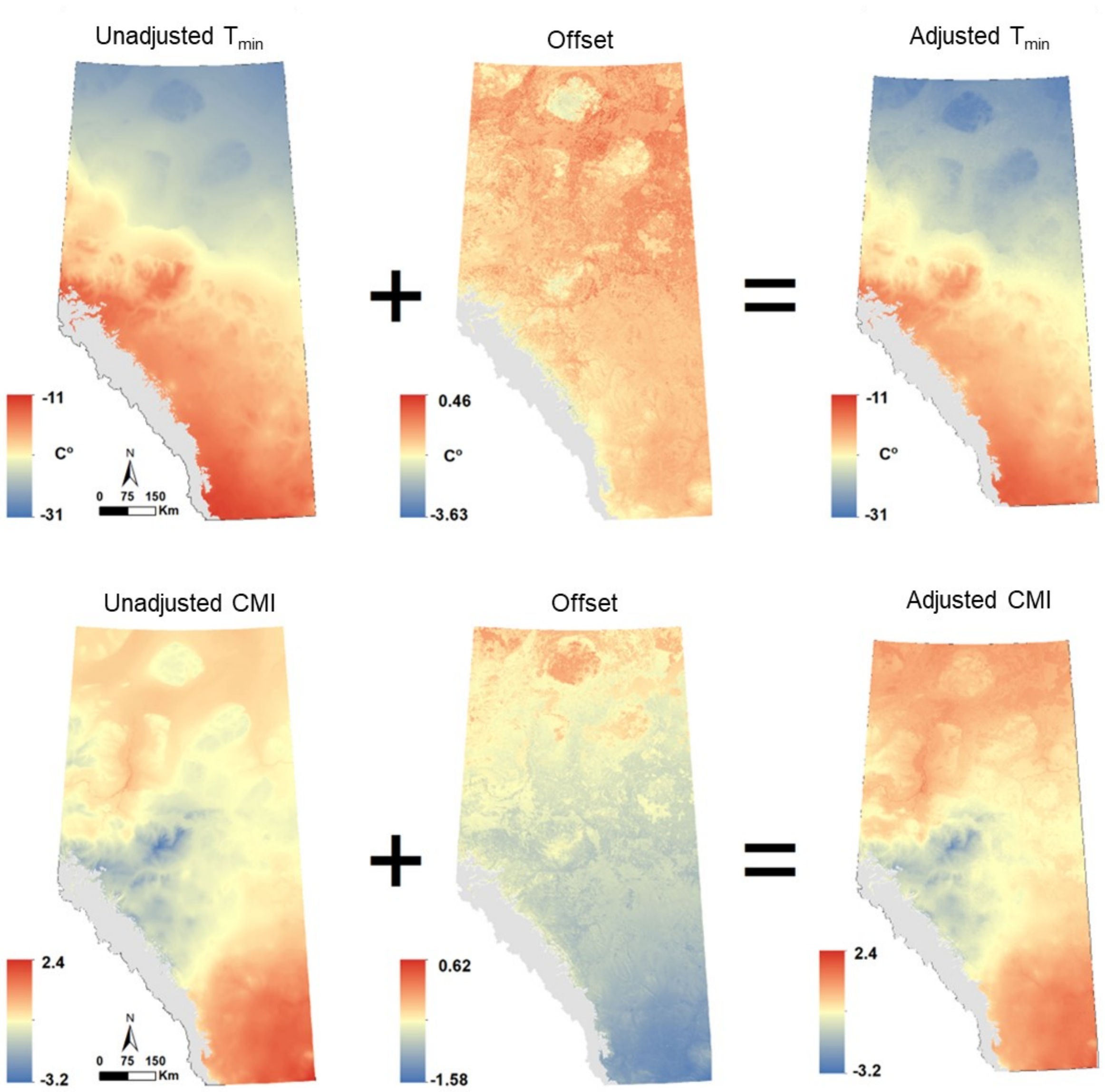


Figure 2.2: Unadjusted, offsets and adjusted minimum temperature and summer climate moisture index (CMI) developed for Alberta, Canada for the period of 1960-1991 normal period.

Results

Relative influence of environmental variables

We observed a range of pseudo-R^2 across species for each set of models, from approx. nearly zero (e.g., Marsh Wren *Cistothorus palustris* – MAWR, White-breasted Nuthatch *Sitta* *carolinensis* – WBNU, Evening Grosbeak *Coccothraustes vespertinus* – EVGR) to approx. 0.70 (Mountain Chickadee *Poecile gambeli* – MOCH). We observed that the explanatory power of models improved using adjusted vs unadjusted climate conditions for 19 and 15 species out of 48 species for the full and climate-only models, respectively (Figure 2.3). The explanatory power of the models was generally low ($R^2 < 0.05$) for 16-18 of species using the full models and for 12-18 when using climate-only models (Figure S2.1). From the habitat groups analyzed, coniferous-associated species showed the largest increase in explanatory power with the use of adjusted climate variables (48% - full model; 30% - climate-only model), followed by deciduous-associated species (20%). Interestingly, the difference in exploratory power changed substantially between full and climate-only models, particularly for coniferous-associated songbirds, where pseudo-R^2 of models using adjusted climate variables declined considerably.

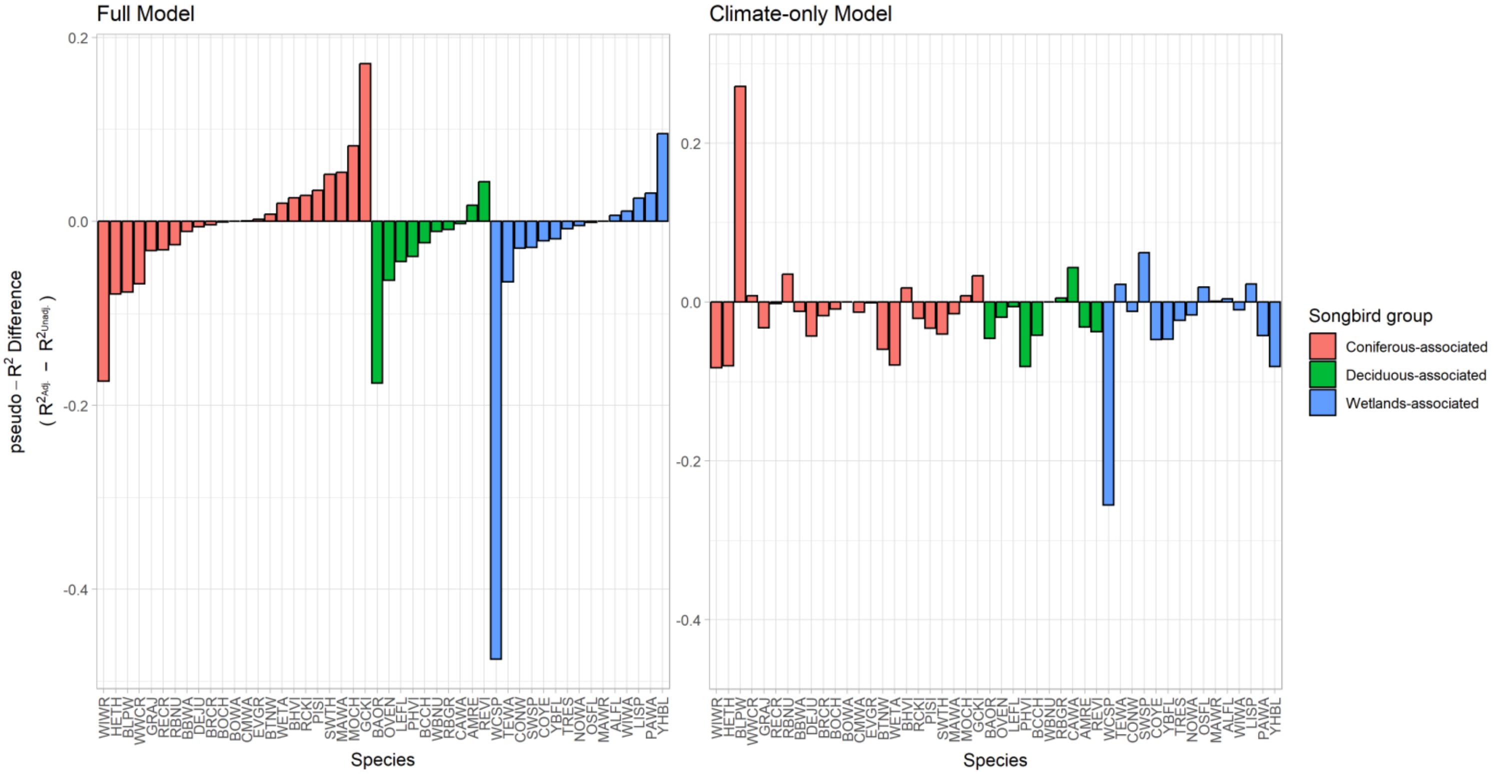
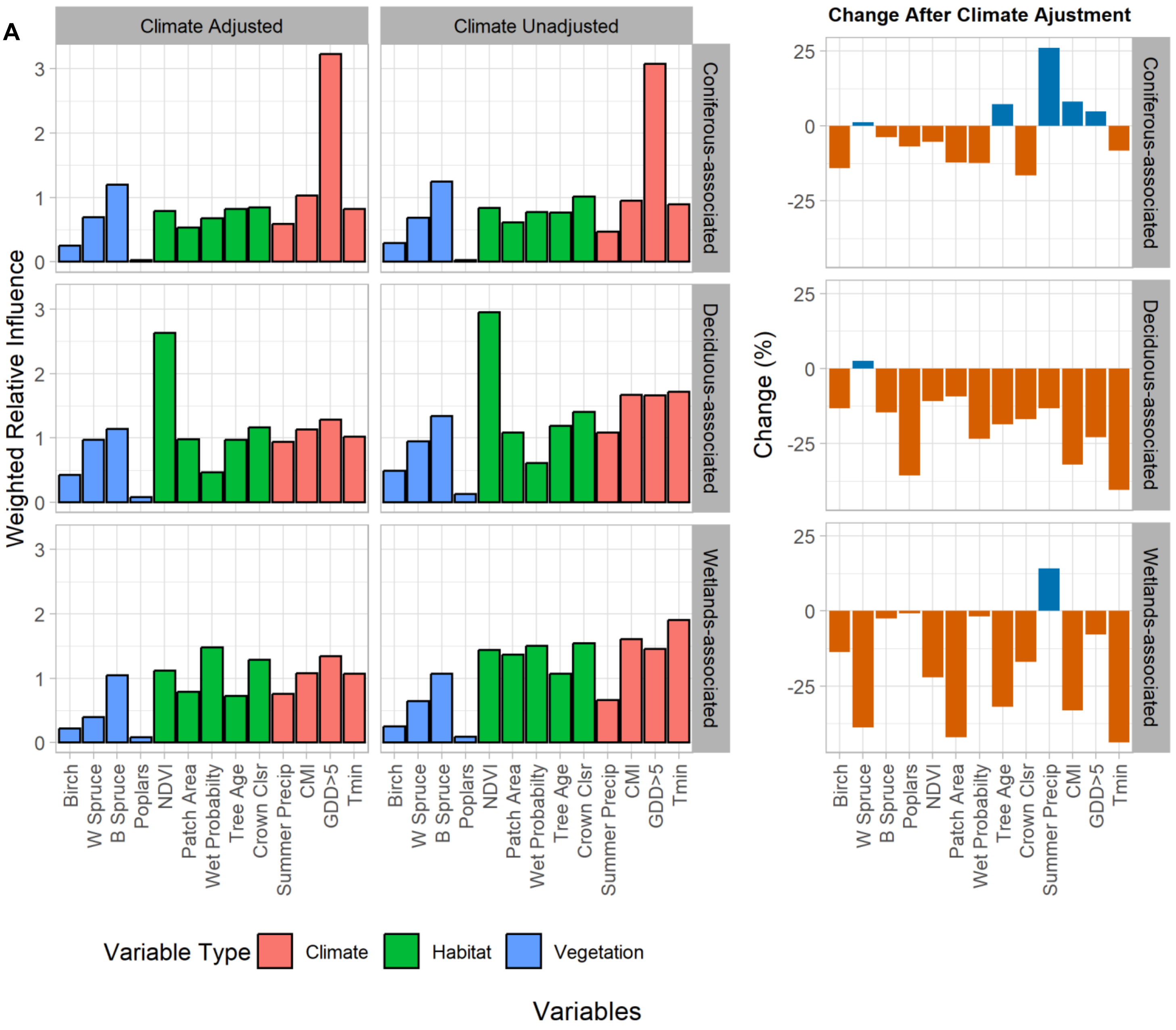


Figure 2.3: Explanatory power of full and climate-only models using adjusted and unadjusted climate variables for songbirds in Alberta, Canada. Adjusted climate variables refer to the topographic downscaling of macroclimate, while unadjusted climate is macroclimate without downscaling. The y-axis shows the difference between pseudo-R^2 of models that use adjusted climate variables and unadjusted climate variables. Species have been ordered by the ratio on the x-axis of the left panel. Full

models incorporate both climate and vegetation variables. Values <0 indicate poorer explanatory power of models using adjusted climate variables than models using unadjusted climate variables.

The relative influence of environmental variables changed substantially in strength for most songbird groups depending on whether adjusted or unadjusted climate variables were used (

Figure 2.4, Table S2.1). Deciduous- and wetland-associated songbirds saw the highest change in influence for climate variables, where adjusted summer CMI dropped in importance by over 31% for both groups, and Tmin by over 39%. Tmin dropped slightly for coniferous-associated species (7%), while summer CMI increased in importance by about 9%. Overall, we also observed that vegetation and other habitat effects decreased in importance after adjusting climate variables, for all groups, but this decline was smaller for coniferous-associated species. Importantly, changes in relative influence varied considerably by species within the same nesting habitat group (Table S2.2 and Table S2.3) and some variables ranked as some of the least important (or most important) after climate adjustment. For example, for Red Crossbill and White-winged Crossbill (coniferous-associated species), summer precipitation changed from the least three important variables to ranked as most important variable after adjustment, but for Cape May Warbler CMI dropped from the top three most important variable to eighth (Table S2.3). We observed similar results for some deciduous-associated species (e.g., Black-capped Chickadee, Ovenbird, Philadelphia Vireo, and Red-eyed Vireo) and wetland-associated species (Alder Flycatcher and White-crowned Sparrow), which showed strong changes in how variables ranked differently after downscaling (both positively and negatively; Table S2.3).


A
Climate Adjusted
Climate Unadjusted
Change After Climate Ajustment
Coniferous-associated
Deciduous-associated
Wetlands-associated
Weighted Relative Influence
Change (%)
0
1
2
3
25
0
-25
Birch
W Spruce
B Spruce
Poplars
NDVI
Patch Area
Wet Probabilty
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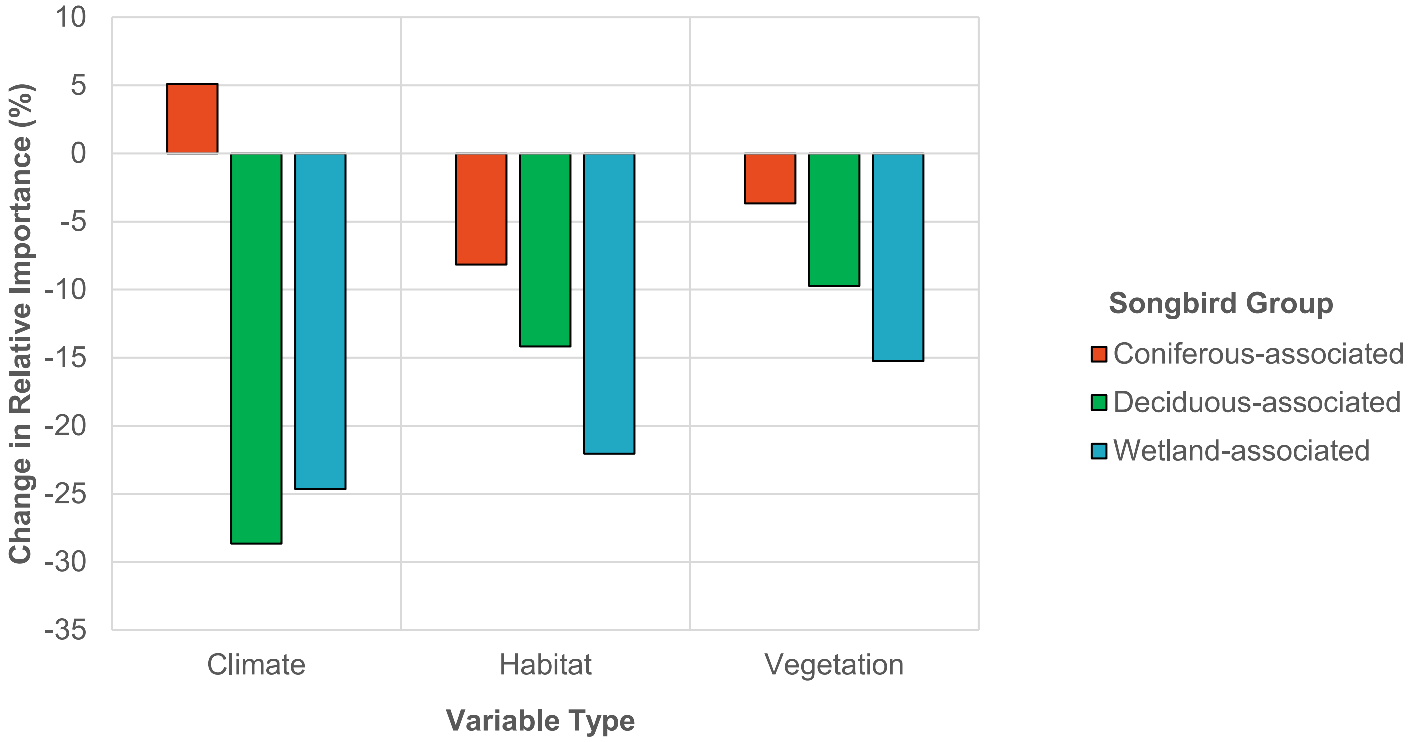


Figure 2.4: Change in weighted relative importance after climate adjustment (mean) of predictor variables (A) and by predictor variable type (B) on songbird groups distribution in Alberta, Canada. The relative importance of each variable was weighted by pseudo-R^2 for each species and then averaged across nesting habitat groups. Results shown are for the full models that incorporate both climate and vegetation variables.

Changes in refugia area

Our predictions of refugia area changed considerably by variables used (i.e., adjusted vs. unadjusted climate), model and between songbird groups. With climate-only models, adjusted climate variables resulted in an increased refugia area of approximately 45% for coniferous-associated species, but decreased refugia for deciduous- and wetland-associated species under a moderate warming scenario (SSP370; Figure 2.5).

The total area of refugia projected by the end of the century indicated a loss of more than 13% of current suitable habitat for all groups and model types (Figure 2.5). Loss in total refugia area was generally higher for climate-only models that used unadjusted variables, but that varied among groups. Coniferous-associated species had the highest loss (58%) predicted with climate-only models (unadjusted) among all groups, while the climate-only model with adjusted variables had smaller loss for that group (21%). We also observed high levels of loss for deciduous-associated species with the climate-only models and unadjusted climate (58%), and smaller loss levels when vegetation variables were included (28% with unadjusted climate and 14% with adjusted climate). In contrast with the other groups, we observed higher losses for wetland-associated species when using climate-only models with adjusted climate (43%), while incorporating vegetation variables and unadjusted climate led to lower loss (16%). Generally, when vegetation variables were included in the models the use of adjusted climate variables resulted in a smaller refugia area for coniferous- and wetland-associated species, but a larger refugia area for deciduous-associated species (Figure 2.5).

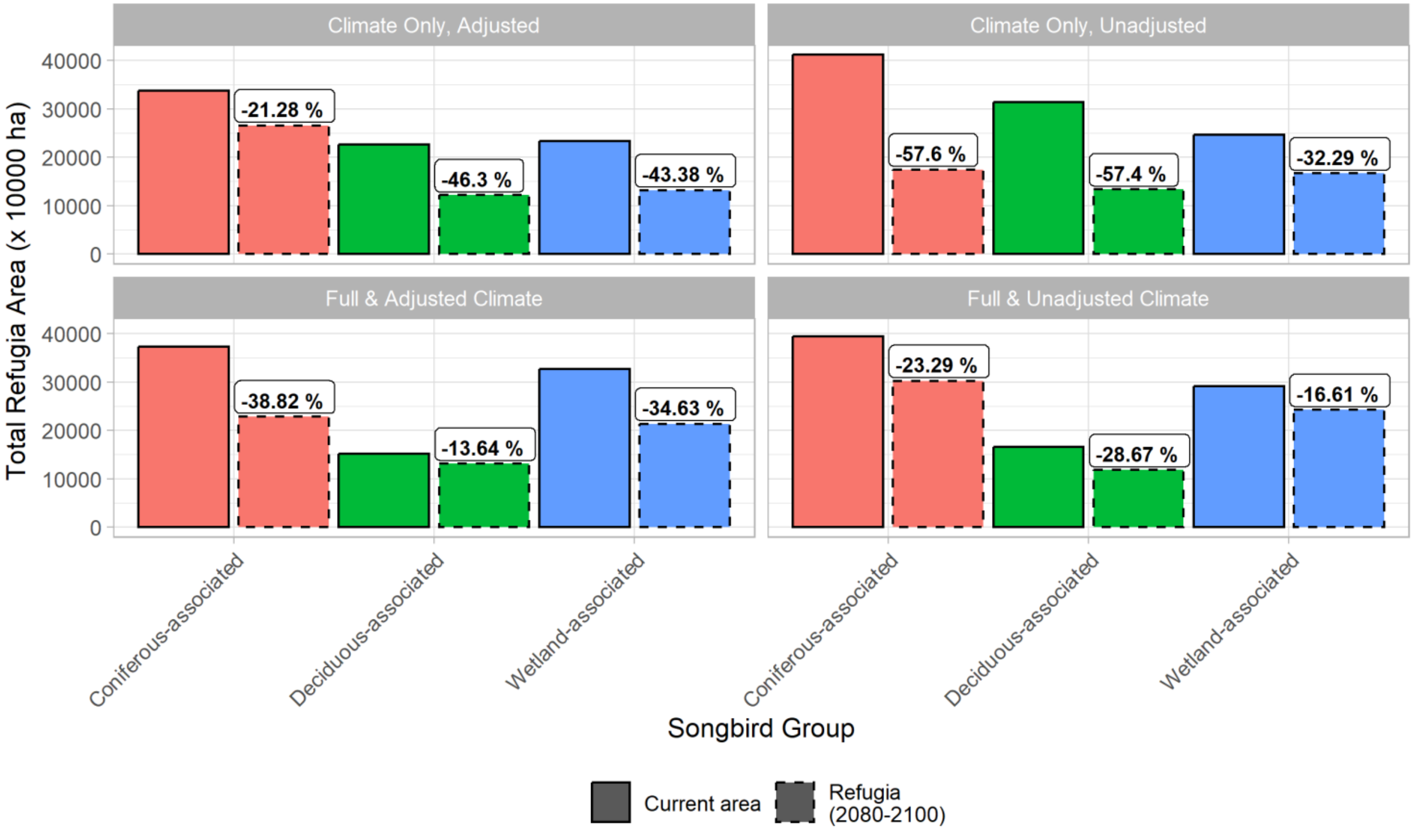


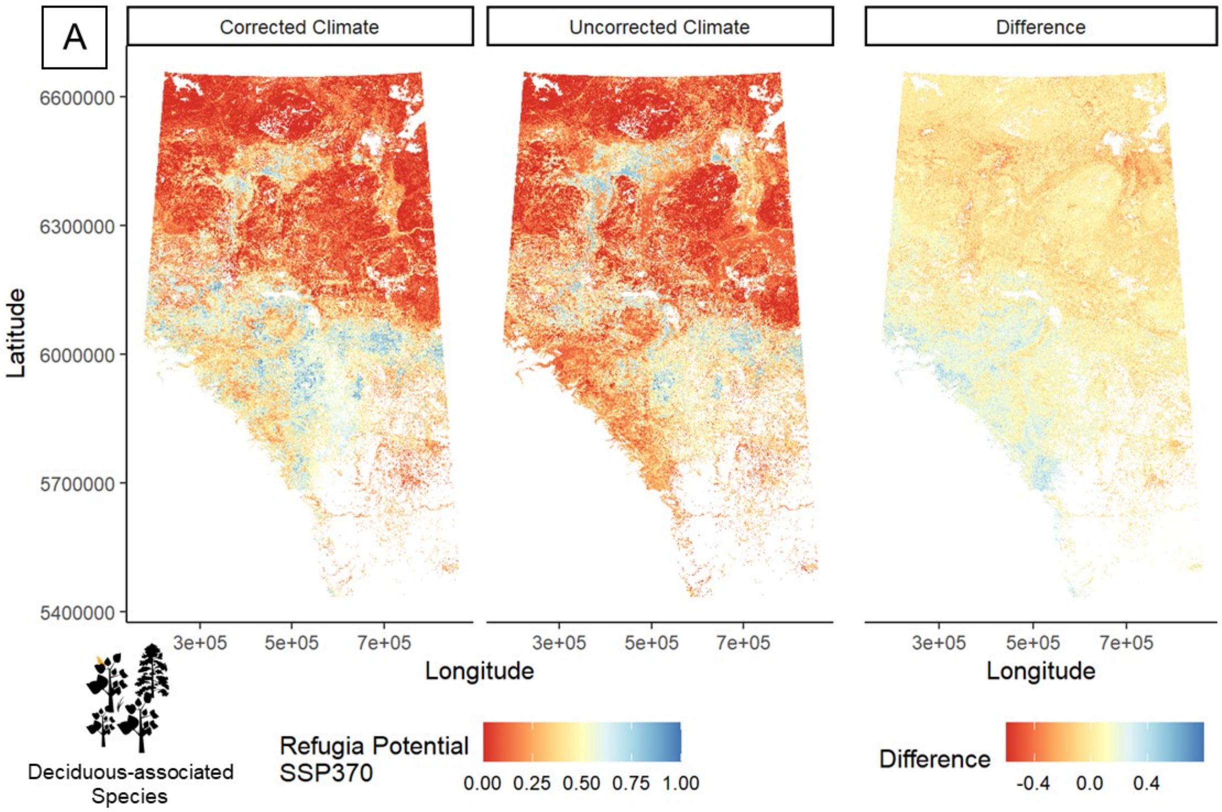
Figure 2.5: Total refugia area per model (climate-only or full – climate + vegetation) and songbird species group in a moderate climate scenario (SSP370). Full models are models that include vegetation and habitat variables, while models that include climate adjusted for local topography and vegetation cover are marked as adjusted, or unadjusted otherwise. Highlighted bars indicate current (i.e., present) total

refugia predictions. Numbers at the top indicate the percentage change in area relative to current area.

Changes in refugia location

Spatial predictions of climate change refugia potential indicated some differences in terms of location of areas with higher and lower overlapping ranges (i.e., high or low refugia potential) depending on which model was used (climate-only vs full models) and whether adjusted climate variables were used (Figure 2.6). Climate-only predictions typically predicted broader refugia potential, while full models were more spatially defined and localized. Climate-only models predicted a higher refugia index for coniferous-associated and deciduous-associated species (mean refugia index = 0.374 and 0.372, median = 0.300 and 0.286, respectively; Table S2.2), while full models predicted slightly higher refugia for wetland-associated species (mean = 0.371, median = 0.286). The frequency of refugia index values was generally right skewed across models and species groups. Within both model types (climate-only and full models), the refugia index was generally higher when using unadjusted climate for coniferous-associated and wetland-associated birds. Generally, the location of high/low refugia potential areas were in the same areas for both climate-only and full models within the same set of climate variables (adjusted vs unadjusted; Figure 2.6).

We found that high refugia potential areas for deciduous-associated species were located along lowland areas in the central and west river valleys (Figure 2.6 (A) and (B)). Our results indicated mid-levels of refugia potential for coniferous-associated species across the boreal biome, with high potential areas being very localized (Figure 2.6 (C) and (D)). Meanwhile, high refugia potential areas for wetland-associated species was mostly located in the north and northwest (Figure 2.6 (E) and (F)). We also found higher discrepancy between predictions that based off adjusted and unadjusted climate variables for species associated with coniferous woodlands and wetlands (Figure 2.6, third column). In general, we also found that the foothills consistently had increased refugia potential when including adjusted climate, while northern Alberta had decreased refugia potential with adjusted climate. The change centroid of refugia potential relative to the current habitat suitability varied across species groups and model types (Figure S2.2). Full models predicted a northward change of 10 km in their refugia centroid when using adjusted variables, and a 21 km change northwest with unadjusted climate variables, while climate-only changes were minimal (<6 km). Centroids for deciduous-associated species moved southward for the full models (25-32 km), while climate-only models with unadjusted climate predicted a northeast change of 25 km. Wetland-associated species had the smallest change in refugia centroid (<1 – 5 km; Figure S2.2).


A
Corrected Climate
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Difference
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Latitude
3e+05
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7e+05
Longitude
Deciduous-associated Species
Refugia Potential SSP370
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1.00
Difference
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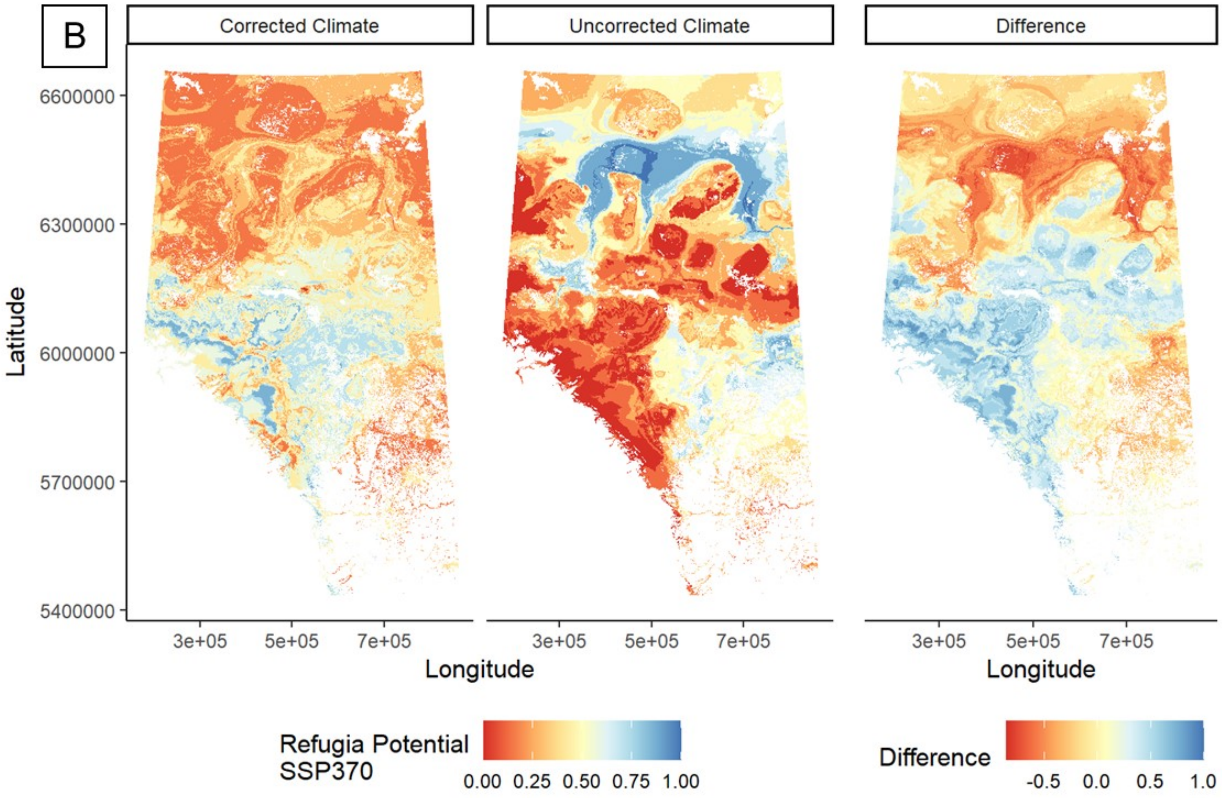
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Latitude
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Difference
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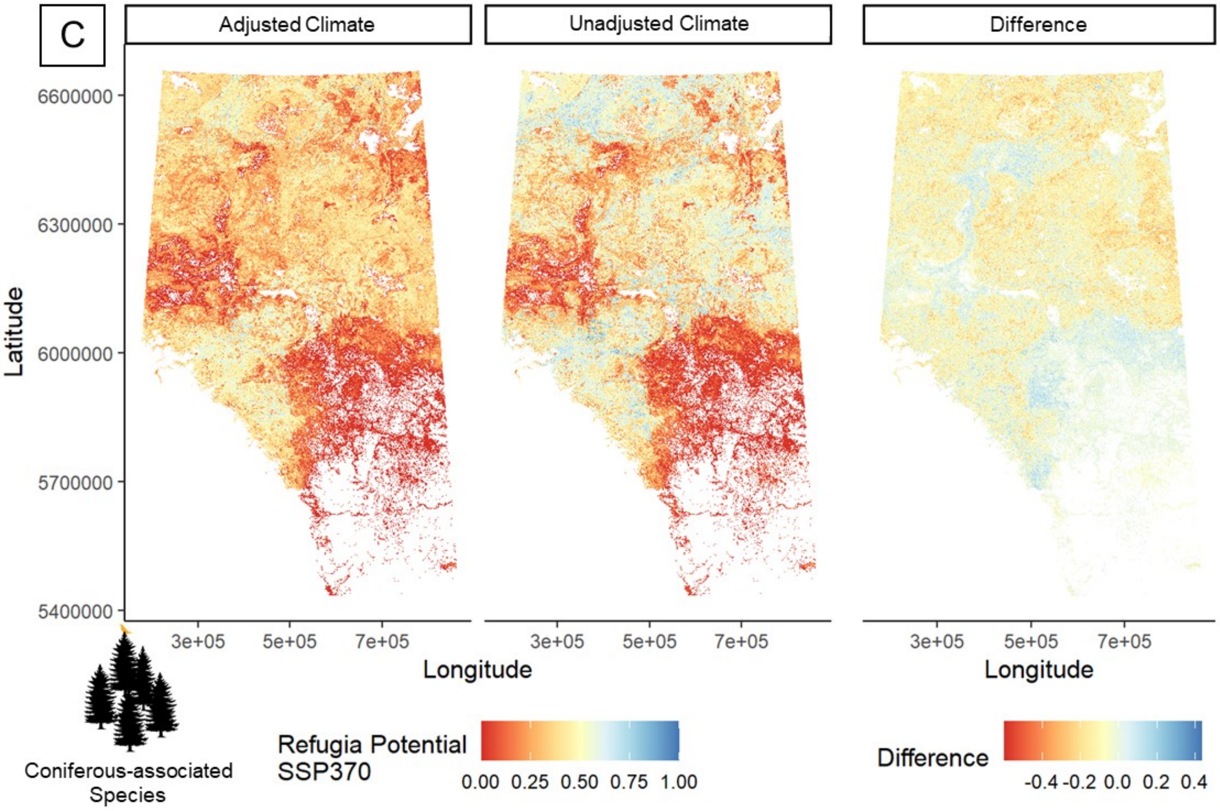
1.0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5e+05
7e+05
Longitude
Coniferous-associated Species
Refugia Potential SSP370
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0.50
0.75
1.00
Difference
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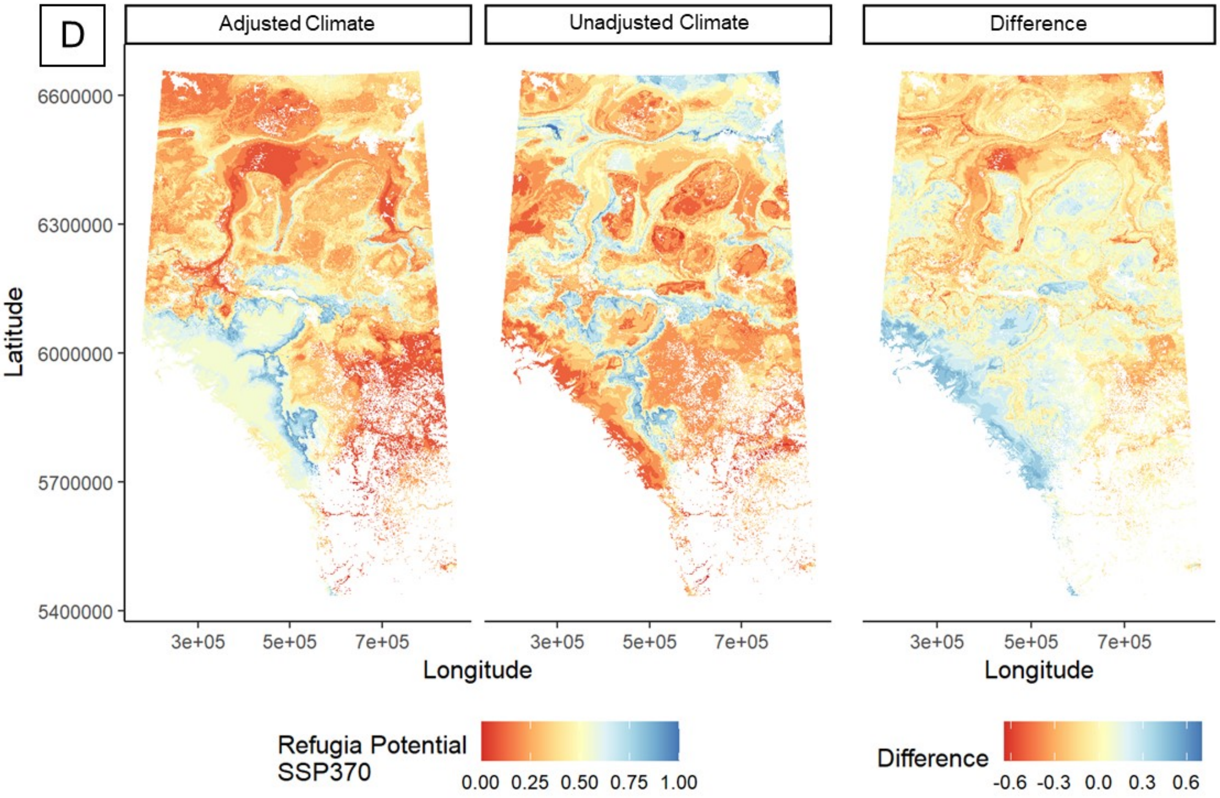
0.0
0.2
0.4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Adjusted Climate
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Longitude
Refugia Potential SSP370
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Difference
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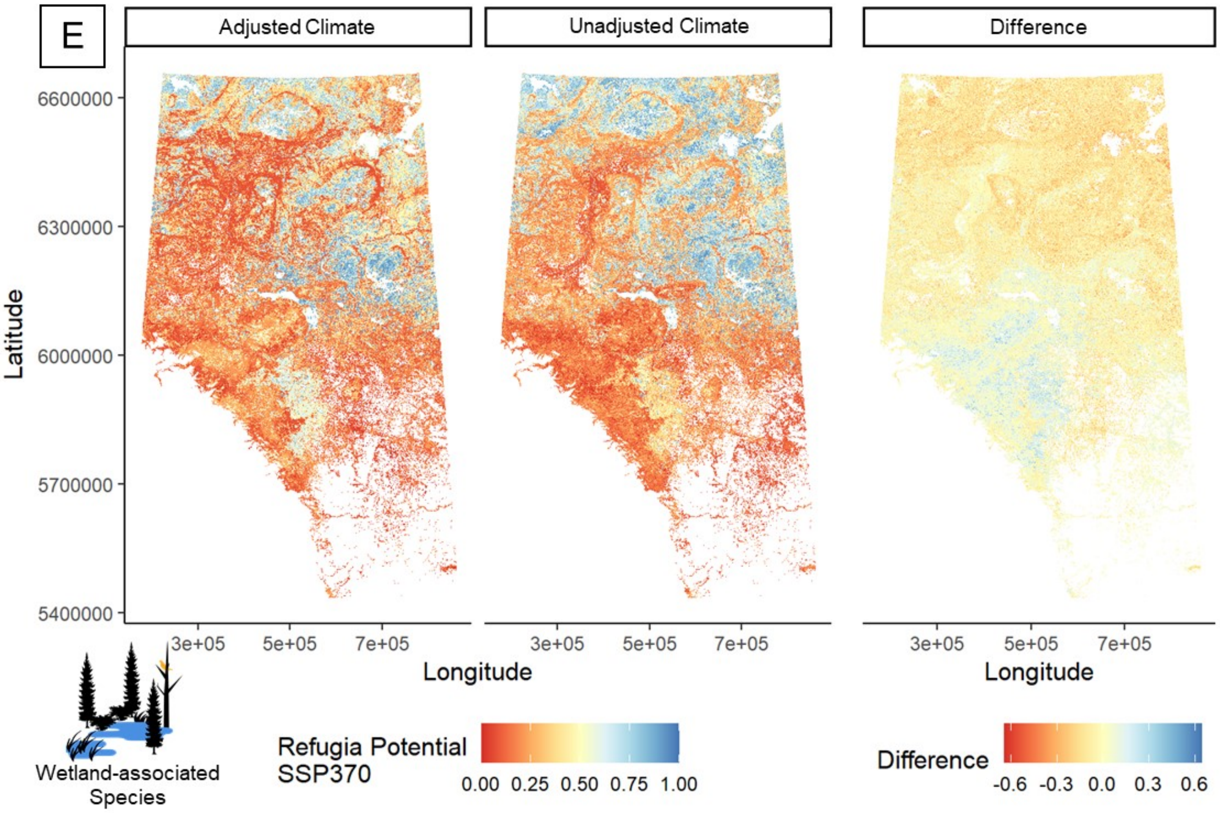
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Adjusted Climate
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Latitude
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Longitude
Wetland-associated Species
Refugia Potential SSP370
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1.00
Difference
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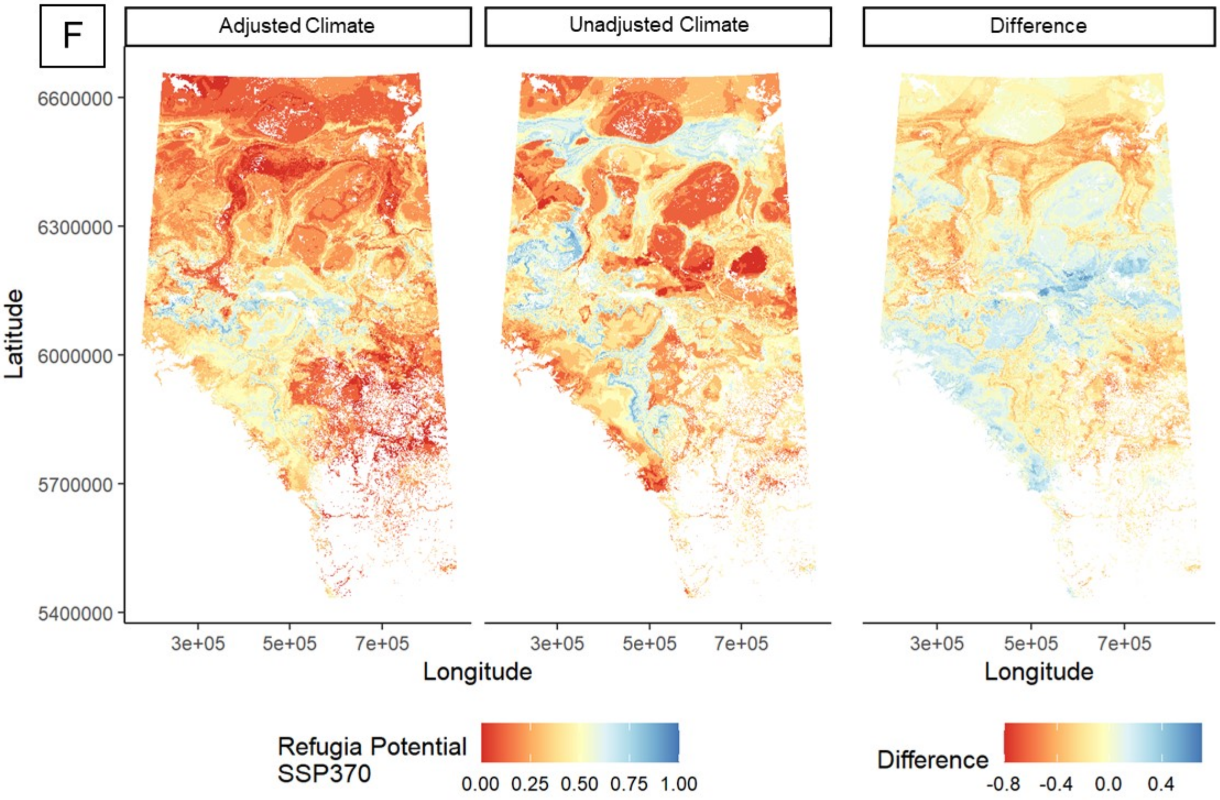
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Longitude
Refugia Potential SSP370
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0.25
0.50
0.75
1.00
Difference
-0.8
-0.4
0.0
0.4

Figure 2.6: Climate change refugia potential for (A-B) deciduous-, (C-D) coniferous-, and (E-F) wetland-associated species in Alberta, Canada. Predictions at the top row for each panel were made with the full model while the bottom row are based on the climate-only models. The first and second columns indicate whether the adjusted or unadjusted climate variables, respectively, were used, while the third column shows the difference between the first and second columns. The values of each map on the first two columns reflect the normalized (from 0 to 1) sum of future species occurrence. Notice that the scale for the difference (third column) is different for each model type. We excluded the Rocky Mountain ecoregion from predictions.

Discussion

Understanding climate-change impacts and effects for refugia at different scales can help identify opportunities for climate adaptation across taxa. Adjusting climate database on local topography and vegetation cover is a primary way to achieve that. Here, we investigated the impact of climate adjustment on local climates and found that the projected distributions and refugia potential for songbirds changed considerably depending on whether climate variables were adjusted to local topography and vegetation cover. Our results indicate that incorporating local climate has impacts on explanatory power of models, the predicted amount of refugia, and on the estimated loss of suitable habitat. Overall, our results suggest that the explanatory power of models improved for <50% of species, suggesting that most of the species analyzed may not be sensitive to local climate. Most of the species that improved in model performance were associated with coniferous forests. The relative influence of climate variables decreased after adjusting for local topography and vegetation cover by over 30% for deciduous- and wetland-associated species (except summer precipitation for the latter), suggesting that climate at broader scales maybe more important for those groups but increase. For coniferous-associated species, the importance of climate variables increased by 6 – 27% (except Tmin). Relative to the current area of distribution, we predicted a loss of at least 13% of suitable habitat across species groups, but that loss varied up to nearly 58% by model (full vs climate-only models), species group, and whether adjusted climate variables were used. This finding not only suggests that some species groups may be more sensitive to local climate (i.e., coniferous-associated species), but it also highlights the overarching importance of vegetation composition on species occurrence.

Relative influence of environmental variables

Climate influences the life cycle of animals at multiple scales. Adjusted climate is more likely to match what a terrestrial organism is experiencing on or near the ground (Bramer *et al.*, 2018), while unadjusted climate variables may be proxies for broad spatial gradients of species distribution. Our downscaling approach considered that adjusted climate is a function of macroclimate (large-scale) and other processes at the local level (local-scale). Our results suggest that topography does influence local climates in a way that can be detected for some bird species because we detected changes in the relative impact of climate variables after adjustment. However, most species in all groups did not show substantial model improvement, suggesting that most species may not be sensitive to local climate. This may be because microclimate conditions become more important for a species when regional climate suitability is low (Massimino *et al.*, 2020), which generally occurs near its range limits (Oliver *et al.*, 2009) and key climate thresholds. Therefore, local climate conditions may have importance for certain songbird groups because macroclimate conditions are already suitable, and downscaling leads to minimal improvement. Conversely, downscaling can improve model performance for plant species, particularly because incorporating microclimate may pick up more of the variation in factors influencing species distribution than macroclimate alone (Storlie *et al.*, 2013; Slavich *et al.*, 2014, but see Stark and Fridley, 2022 for contradictory results). We observed that the explanatory power of models increased only for a few species within each group (and only for the full models) after adjusting climate for site-level topographic effects, but slightly more so for coniferous-associated species (about half of the species). In general, this indicates that only a few species were sensitive to local climate conditions in this region, including Golden-crowned Kinglet (*Regulus satrapa*), Mountain Chickadee (*Poecile gambeli*), Magnolia Warbler (*Dendroica magnolia*) and Swainson's Thrush (*Catharus ustulatus*), some of which have been previously indicated to be sensitive to climate at local scales (Kim *et al.*, 2022).

We observed that the relative influence of climate variables dropped substantially after adjusting for local topographic and tree cover effects for deciduous- and wetland-associated songbirds. This suggests that these groups may be less sensitive to the influence of local climate conditions and more influenced by climate at a regional (or macro) scale, as climate adjustment reduced the variability explained by most climate variables, though that varied by species. Overall, these two groups seem to be driven by local habitat characteristics (i.e., vegetation and habitat) that are not strongly climate linked. For wetland-associated species, this is probably the result of the relatively low topographic diversity and flatness of where wetlands are typically found in the Western boreal (Schneider, 2013). Moreover, local climate in wetlands may vary substantially at very small scales, depending on wetness conditions and moss composition (Słowińska *et al.*, 2022; Kolstela *et al.*, 2023 - preprint), which are processes not captured in the scope of this paper. Conversely, deciduous-associated species may be influenced by factors beyond climate. For instance, many species in that group have strong associations with shrub cover, which is generally higher in deciduous-dominated forests, and results in higher food abundance relative to coniferous forests (Werner, 1983; Willson and Comet, 1996). These results may also emerge because spatial distribution patterns are associated with other factors than climate *per se*. For instance, factors like dispersal and interspecific interactions may result in distribution gradients that broadly follow climate (Godsoe, Franklin and Blanchet, 2017; Stephenson *et al.*, 2022). Nevertheless, changes in relative influence of climate variables varied considerably between species within the same group.

Our results suggest that local climate conditions may be more influential for coniferous-associated species in general, as well as some wetland- and deciduous-associated species for which climate variables became more important when we adjusted climate to the local scale. For instance, we found that effects of summer climate moisture index (CMI) at smaller scales (e.g., site-level) were more important than unadjusted summer CMI effects. Annual CMI is one of the strongest predictors of the range of coniferous forests in the boreal biome, which reflects the fact that western boreal conifers are moisture-limited (e.g., Hogg, 1994). Climate adjustment may inevitably lead to patchier CMI patterns, which coniferous-associated species appear to follow, suggesting that this group is particularly sensitive to moisture balance. Moreover, we also observed a small decrease in the impacts of other variables (e.g., vegetation and other habitat variables) for this group, which in combination with the changes in climate suggests that these variables are less important because the habitat characteristics they respond to are better captured by downscaled climate. Overall, these results seem to corroborate our hypothesis that coniferous-associated songbirds and the habitat they depend upon within our study region might be more sensitive to the influence of local climate conditions. Despite the mean changes in relative importance per group presented here, our results do highlight that climate downscaling affects species differently. Those differences could be driven by differences in niche breadth, range size, and latitudinal limits. For example, population growth changes depending on a species' position relative to its thermal range (Jiguet *et al.*, 2010). This reinforces the notion that co-occurring species may respond to climate change differently (Williams and Jackson, 2007).

Changes in Refugia Area and Location

Species response to climate at different scales is conditional on species-habitat associations (Suggitt *et al.*, 2012). Therefore, climate downscaling can increase or decrease climate suitability depending on how species respond to climate extremes (Slavich *et al.*, 2014). In our study, all species had predicted refugia areas smaller than their current distribution, but the magnitude of change varied depending on climate variables used (adjusted or unadjusted) and between model types (climate-only vs full). In general, our results suggest that despite having the largest area of current distribution, coniferous-associated species had the greatest loss in suitable habitat (21-58% loss, relative to their current distribution area), followed by deciduous- (14-58%) and wetland-associated species (16-43%). We predicted more refugia for coniferous-associated and deciduous-associated species when we used adjusted climate variables, which partially supported our expectation. The results for deciduous-associated species contradicted our expectations that climate adjustment would make no difference for this group. That could be related to the fact that deciduous-associates species are generally projected to increase in Alberta (Stralberg *et al.* 2015).

Refugia for wetland-associated species seemed to be independent of climate adjustment, because the amount of refugia did not change if habitat variables were included, which suggest that this group is mostly driven by macroclimate and somewhat insensitive to local climate. This, and the flatness of wetlands suggests that this group is prone to respond to macroclimate variation and may not necessarily benefit from climate buffering from topography, at least at the scale we analyzed here. In contrast, macroclimate models (i.e., unadjusted predictions) resulted in higher refugia potential for wetland-associated birds. This may suggest that the distributions of wetland-associated species are driven more by hydrology than by climate. It is also important to note that wetlands, especially when connected to groundwater sources, may have high refugia potential via water storage capabilities (Kettridge et al. 2016) that can regulate local climates in other ways, not captured in our study.

For coniferous-associated species, climate-only model predictions with unadjusted climate resulted in a higher mean refugia compared with the other models, but the loss of suitable habitat was lower when we used adjusted climate. This suggests that this group is more sensitive to the local climate variability that is associated with topography and canopy cover and results in locally cooler and moister conditions (Estevo et al. 2022, Hogg et al. 1994). It is known that growth of white spruce, one of the most common tree species in the western boreal forest, responds strongly to variations in moisture balance, as indicated by the climate moisture index

(CMI) (Hogg et al., 1997), which may relate to high importance of adjusted CMI for this group. However, it is important to note that climate-only models with adjusted climate had, in general, lower explanatory power than models with unadjusted climate.

In general, our results provide partial support for recent work that incorporates microclimates into species distribution modelling. Climate downscaling has been shown to, in general, identify more suitable habitat when climate-forcing factors such as topographic processes at small scales are incorporated, reducing rates of projected biodiversity loss (Slavich *et al.*, 2014) and resulting in greater species persistence under climate change (Randin *et al.*, 2009). Other studies have found small or no differences in predicted area of occurrence between downscaled and macroclimate scenarios (Storlie *et al.*, 2013). It is important to account for methodological differences, particularly around variable selection, predictors and response variables (Austin and Van Niel, 2011). Our approach summed the number of pixels with overlapping distribution for individual species and then lumped them by nesting habitat, which could have led to different results if we had considered all species, or used different nesting habitat groups (e.g., Figure 2.5). On top of that, it is important to note that some of the studies that incorporated microclimate (or site-level climate forcing-factors) used sessile species as their model organism (Trivedi *et al.*, 2008; Austin and Van Niel, 2011; Slavich *et al.*, 2014). Considering the vagility of birds and the fact that they experience a wide range of climate throughout their life cycle (e.g., migration, distinct wintering and breeding territorial grounds), birds' sensitivity might not be as strong as plants'. Moreover, climate effects may well vary by species depending on their niche breadth, with specialists being more vulnerable (Jiguet *et al.*, 2007; Davey *et al.*, 2012). It is possible that factors beyond climate, e.g., competition and other interspecific interactions, may have more influence on the distribution of all groups and lead to local scale variation that is not explained by local climate (or habitat) alone (Araújo and Luoto, 2007).

We also found similar predictions of high/low refugia areas between climate-only and full models, where the location of high/low refugia potential areas generally coincided. The direction and distance of the centroid of refugia potential for coniferous- and deciduous-associated species changed depending on the model and type of climate variable used (adjusted vs unadjusted). Assuming zero dispersal, our results indicated that using adjusted climate variables led to shorter shifts of their suitable habitat centroid, suggesting that the persistence of refugia may be higher once local climate effects are incorporated. The higher persistence and shorter changes in the centroid of suitable habitat can be attributed to higher variability in climate on the landscape and suggests that the adjusting climate conditions created further thermal opportunities for occurrence and for species to track optimal climate conditions (Stark and Fridley, 2022). The directionality of the change in centroid from currently suitable habitat can be mostly related to the vegetation that the different groups are most associated with; it also indicates where refugia are in relation to their current distribution. For full models that accounted for vegetation, the north/northwest centroid change for coniferous-associated species follows a general trend for bird distribution in North America (Price et al. 2013, Stralberg et al. 2015, Dunn and Møller, 2019). This northern centroid change indicates that refugia might be in northern latitudes in Alberta, which also have a higher prevalence of coniferous trees. For deciduous-associated species, which showed a southward centroid change for the full models, the result could be driven by the higher prevalence of deciduous trees in the grassland-boreal ecotone (*i.e.*, boreal Parkland; Hogg 1994). This southward shift suggests that refugia might be in the southern margin of their current distribution. The larger changes in distribution centroid happened mostly with the full model, particularly with the use of unadjusted variables. Climate-only models, instead, predicted only small changes relative to current suitable habitat across species. This small change seems counter-intuitive because we held vegetation constant in future predictions, which should have constrained long changes in distribution for all groups. However, these results may be consistent with the fact that conifer-associated species occur mostly in the north and that not much shift was involved according to the unadjusted models. The results may also highlight that from a purely climatic perspective, only small variations may be expected in refugia location. This level of variation between climate-only models and models that incorporate vegetation further stresses the need to predict future vegetation change in tandem with species occurrence. For wetland-associated species, changes were minimal across all model and variable types (adjusted or unadjusted climate), suggesting that other factors beyond climate may be more important for this group. Our approach to define a single location (centroid) to define the entire distribution of a group of species is thus an oversimplification of the actual change in distributions, and clearly ignores the variability of areas with higher refugia potential and ignore the potential for dispersal to novel conditions. These ‘hotspots’ in refugia potential likely have higher weight in determining the actual direction and spatial shift of refugia potential.

Both climate and vegetation variables exert an important role in the distribution of songbirds, but teasing apart each of these effects is difficult. In general, incorporating environmental factors beyond climate should result in better, more detailed current predictions. However, as climate and vegetation conditions decouple over time, future projections will be constrained by holding vegetation variables constant. Conversely, climate-only models may exaggerate the role of climate *per se*, resulting in projections that are overly exaggerated.

We do urge caution when interpretating our results precisely because none of the vegetation variables used here were projected into the future. Incorporating additional habitat features (i.e., vegetation) may inevitably absorb a lot of the variance otherwise explained by climate. Previous work that examined the impacts of local effects on climate and on species distribution did not project changes to habitat and left it static over time (Randin *et al.*, 2009; Slavich *et al.*, 2014). Incorporating forest change simultaneously to wildlife projections has proven to be difficult given the complexity of the models and the level of assumptions about land cover change (Lalechère and Bergès, 2022), so further development is needed. Stand-replacing and wide-ranging wildfires are pervasive agents of forest change in the boreal biome (Stralberg, Wang, *et al.*, 2018), which makes predicting vegetation in a climate change even a more difficult. Nonetheless, we believe that our full models may be underpredicting refugia potential because our approach included mainly a process of climate overlap. Lastly, how long refugia will last remains uncertain in the literature but there is agreement that refugia persistence may vary overtime (Stralberg *et al.*, 2020), which adds yet another layer of complexity and caution when interpreting our results.

Conclusions

We conclude that different groups of species, and their intrinsic relationship with their habitat, plays an important role into how they are affected by local climate, and therefore, how much refugia is available to them. An interesting interface between habitat, local climate and macroclimate seemed to drive the amount of refugia predicted for coniferous- and deciduous-associated species. For coniferous-associated species, local climate played a bigger role when vegetation structure and composition variables were not included, while deciduous-associated species responded the opposite way. Finally, wetland-associated species seem to be more influenced by macroclimate, regardless of habitat effects. Meanwhile, changes in distribution of suitable habitat for these groups may indicate where their higher refugia potential areas could be located and be indicative where managers could target conservation efforts. For instance, northern latitudes with high refugia potential in Alberta could be protected for coniferous-associated species, and similarly in the southern margin of the current distribution for deciduous-associated species.

Including attributes of the habitat that wildlife inhabit into species distribution models, such as composition, age, productivity, may provide further detail into refugia identification.

These attributes will inevitably be affected by end-of-century warming to some degree (Stralberg *et al.*, 2018), which should be incorporated in refugia predictions as well. For example, climate change has already induced changes in forest composition and northward shift of the boreal biome (Berner and Goetz, 2022). Forest change is an essential aspect of the identification of refugia for forest-dependent species and should therefore be incorporated into SDMs. Therefore, we encourage future studies in refugia to look at the impacts of both climate at large and small scales, as well as other important habitat factors that could contribute to the distribution of species.

Acknowledgements

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Chapter 4 – Disentangling the role of climate and vegetation on boreal songbird habitat

Summary

Both direct and indirect effects of climate on birds are important considerations in the context of conservation and climate-change adaptation, such as climate-change refugia, but indirect processes are rarely quantified in ecological studies. Structural equation models (SEM) have emerged as a technique to resolve multivariate relationships to quantify and tease out direct and indirect effects of interrelated variables. We sought to disentangle the direct and indirect role that climate plays in defining habitat for boreal trees and boreal songbird species, which may inform our understanding of bird responses to climate change in boreal North America. We surveyed boreal songbirds in Alberta, Canada between 2012-2018. Then, we used a combination of occupancy models and SEM to understand the drivers of occurrence of 16 songbird species and biomass of trees as a function of climate, tree species composition, and habitat structure within a single modelling framework. We found that moisture (climate moisture index – CMI) (mostly positive) and growing degree days above 5 ^{o}C were the strongest predictors of spruce trees, 3-4 times larger than the effect of May to September, while winter minima had consistently negative effects across tree species. After grouping songbird species by nesting habitat preferences, we found bird occurrence was driven primarily by vegetation characteristics more than climate. Coniferous- and wetland-associated species were particularly influenced by spruce (*Picea glauca* and *Picea mariana*) biomass. Somewhat surprisingly, the influence of climate was mostly direct, rather than indirectly mediated through vegetation, suggesting that other physical site factors will play an important role in species' responses to climate change. The most important climate variables across species were mean summer precipitation and annual climate moisture (potential evapotranspiration - precipitation). For deciduous-associated bird species, vegetation characteristics were more limiting than climate, suggesting this group could benefit from the expansion of hemi-boreal climates. Biomass of spruce trees were the strongest mediators of the indirect effects of climate. Our results suggest that climate change impacts on boreal birds will manifest via direct effects on their resources (e.g., food and habitat) rather than physiology as well as via indirect effects on vegetation. Our results suggest the potential for rapid change in boreal songbird communities, given the strong direct effects of climate relative to other factors.

Introduction

The distribution of species is determined by a combination of biotic and abiotic factors, which can influence species directly or indirectly, and at different scales (Begon and Townsend, 2020). Perhaps the most fundamental aspect of species distributions is how they are shaped by climate conditions (Guisan and Thuiller, 2005; Thuiller *et al.*, 2008), an idea studied extensively by Alexander von Humboldt (Pausas and Bond, 2019). Humboldt in his foundational work *On the Distribution of Plants* (1817) aimed to understand the underlying causes of distribution of plants on the globe and attributed the uneven distribution of plants in mountain regions to the influence of climate. Humboldt's work laid the basis for modern conceptualizations of niche theory (Schrodt *et al.*, 2019). As established by niche theory, the geographic range of a species consists of regions to which the species has been able to disperse, and where abiotic and biotic factors favour its persistence (Gaston, 2003). Species ranges are often defined by a suite of macroclimatic conditions that constrain their physiology (Guisan and Thuiller, 2005). Within a species range, occurrence also depends on climate conditions at finer and more local scales, where interspecific interactions and landcover become increasingly important predictors (Guisan and Thuiller, 2005). These local conditions affect vital rates such as recruitment (Briga and Verhulst, 2015), as well as species energy budgets (Porter, 2002), ultimately leading different populations to be locally adapted (Anderson and Song, 2020; Dunn and Møller, 2019).

In the absence of disturbance, species assemblages are generally expected to remain in equilibrium with macroclimate, if climate does not change too quickly (Price *et al.*, 2013). Paleo records show that many tree species in North America historically occupied areas well outside their current ranges and have spread north due to warming of the continent in the past, highlighting large scale climate controls (18–11 ka, Dyke, 2007). Currently, distributions of the main coniferous tree species of the western boreal forest, particularly white spruce (*Picea glauca*) and black spruce (*P. mariana*) are thought to be limited by moisture balance (Hogg, 1994) because climatic conditions are crucial for establishment and during the early developmental stage for boreal coniferous trees. For instance, white spruce seedling development and growth is higher in moist environments, relative to drier and hot conditions (Hogg and Schwarz, 1997). White spruce mortality has increased with increasing frequency of droughts in Western Canada (Peng et al., 2011) and growth is limited during excessive drought and warm conditions (Barber et al., 2000; Chen et al., 2017). Within their range, boreal tree occurrence is also influenced by topo-edaphic conditions such as soil texture, sand and clay content, pH, and surficial geology, all of which influence nutrient availability and water flow (Hamel et al., 2004). Black spruce often has a patchy distribution related to acidic and nutrient poor soils (Krause, 1998), and can grow where the water table is high (Lieffers and Rothwell, 1987), but is generally outcompeted by white spruce and aspen (*Populus tremuloides*) in rich soils (Wirth *et al.*, 2008). In addition, topography can directly influence trees when it interacts with climate, for example in areas with low sun exposure (e.g., north facing aspects), which leads to cooler microclimates that favor the establishment and persistence of heat-sensitive trees (Estevo et al., 2022).

Local and regional distributions of mobile endotherms such as birds may be less bounded by climatic conditions because of these species' wider physiological tolerance, suggesting a smaller role of climate variables in defining bird niches (Buckley, Hurlbert and Jetz, 2012). Still, it is important to distinguish direct and indirect effects of climate in an endotherm's distribution. On one hand, climate can constrain physiology directly. Under the "physiology hypothesis," birds are limited by climate because of energy availability, which is used to maintain their body within their thermoneutral zone (Currie *et al.*, 2004; Buckley, Hurlbert and Jetz, 2012). There is growing evidence that extreme weather and changing average climate conditions can directly affect recruitment and fecundity of birds, ultimately affecting population growth and demography (Fisher *et al.*, 2015; Dunn and Møller, 2019). The impacts can also be seen at larger scales, such as shifts in entire species ranges, and may indicate that thermal tolerance, despite birds' physiological plasticity, must be considered (Buckley, Hurlbert and Jetz, 2012; Khaliq *et al.*, 2017). On the other hand, climate may influence species indirectly by affecting resource availability, competition, and breeding habitat (Buckley, Hurlbert and Jetz, 2012; Dybala *et al.*, 2013; Engler *et al.*, 2017; Dunn and Møller, 2019). This indirect influence on species can be classified as a "resource hypothesis", where climate influences birds via trophic relationships, mediated by vegetation (Buckley, Hurlbert and Jetz, 2012; Ferger *et al.*, 2014). Moreover, the effects of climate on bird occurrence can be multifaceted, with both physiological constraints and indirect processes affecting their resources and habitat. For instance, topographic variation and its associated effects on local climate (Estevo et al. 2022) may not affect bird distributions directly, but it may have strong impacts on landcover, thereby influencing bird habitat suitability indirectly. Both hypotheses are plausible and supported (Hurlbert, 2004; Kissling, Rahbek and Böhning-Gaese, 2007; Menéndez *et al.*, 2007; Ferger *et al.*, 2014), suggesting that climate influences species in a variety of ways.

In North America, anthropogenic global warming is predicted to shift climate conditions outside the current range in many biomes (Rehfeldt et al. 2012, Stralberg et al., 2019). Therefore, to maintain equilibrium with their climate niche, many bird species will need to shift their range poleward and/or upslope (Hickling et al. 2006; Mason et al. 2015). However, the extent to which bird habitat will be affected by lags in vegetation growth remains uncertain (e.g., Stralberg et al. 2018), and disentangling the effects of climate and other variables is challenging. Structural equation models (SEM) have emerged as a technique to resolve multivariate relationships and to quantify direct and indirect effects of interrelated variables

(Grace, 2006). SEMs are probabilistic models that unite multiple variables and response variables in a single framework. They allow users to quantify indirect or cascading relationships that would otherwise go unnoticed by any single model (Grace, 2006). For instance, consider the hypothetical distribution of a bird species that is negatively affected by both tree abundance and temperature. Here, the resulting indirect effect of temperature on the occurrence of this bird occurs because temperature also impacts the tree. This is a consequence of cascading relationships between climate and the bird. This indirect process is intuitive but rarely quantified in ecological studies. In addition to vegetation composition, the structure of habitat is also important to birds and can be affected by many processes (Ferger *et al.*, 2014). Patch size can affect perceived quality for birds by influencing interspecific interactions such as predation, and by improving colonization vs. extirpation potential, therefore influencing avian occupancy (Morante-Filho et al., 2021). Forest greenness, typically measured via the normalized difference vegetation index (NDVI), can be indicative of forest health (Wang et al., 2004, 2001) and has a climatic component. Therefore, bird distributions can be influenced by an array of abiotic and biotic variables that may improve the performance of species distribution models.

Both direct and indirect effects of climate on birds are important considerations in the context of conservation and climate-change adaptation. An approach to climate-informed conservation is to delineate climate-change refugia (Stralberg et al., 2020) – i.e., areas relatively buffered from climate change (Morelli *et al.*, 2016). At a macro scale, climate-change refugia can be identified based on climate envelopes, wherein areas in which current and future distributions overlap are taken as indicative of their refugia potential (Stralberg *et al.*, 2018). Other approaches also take into consideration local terrain variation and ecosystem processes that are indicative of high ecological inertia, and therefore delay climate-driven transitions (Johnstone et al. 2016, Stralberg et al. 2020). From that perspective, species niches may include a wide range of climatic conditions, such that it responds differentially to climate change throughout its range. However, climate-driven factors such as vegetation may be more important than climate *per se* for bird habitat. In essence, one could expect that local habitat conditions rather than climate directly are bigger drivers (Morante-Filho et al., 2021). The question is, are animals inhabiting forests mostly because of climate conditions or are vegetation-based habitat conditions (e.g., food, shelter, etc.) more important to them? At the same time, the drivers of habitat suitability for the trees that birds depend on could be different or even independent from those that drive habitat suitability for birds, but they are probably not mutually exclusive. Disentangling these processes is difficult and remains a major challenge for species distribution modelling (Grace 2006). In the case of boreal-breeding birds, we hypothesize that the conditions (i.e., composition and structure) of boreal forests that birds occupy are more important than climate *per se*.

In western Canada, existing local climatic conditions allow forests to persist in valley bottoms and shaded slopes within the transition zone between the northern boreal biome and the southern prairie biome (Estevo et al. 2022). Southern forest patches within the prairie biome are similar in some respects to prevailing vegetation conditions in the boreal biome and may be representative of what future northern forests may look like in the future. They include the same tree species (e.g., white spruce, aspen, birch (*Betula papyrifera*), have high crown closure, and a thick understory, but differ in context because of their position (southern latitudes), isolation, size and matrix (cropland/grassland). Yet, whether these relict patches (contemporary refugia) hold any value for boreal birds, and the specific factors that limit bird occurrence (or not) in these places is unknown.

We sought to disentangle the role that climate plays in defining habitat for boreal songbird species. More specifically, our objective was to understand the direct and indirect limiting factors for songbird occurrence in boreal North America, which may inform our understanding of bird responses to climate change. We investigated the direct and indirect environmental factors that limit bird occurrence, while simultaneously modelling the relative biomass of major boreal trees in a single statistical framework, across the boreal-parkland-grassland transition zone in western Canada.

After classifying birds in different groups based on their nesting habitat, we (i) compared the “physiology” and “resource” hypotheses with respect to the occurrence of different songbird groups by comparing the strength of influence of the direct and indirect effects of climate; and (ii) compared the total effects of climate vs. tree composition, while controlling for vegetation structure. We hypothesized that tree species that are more limited by temperature and moisture conditions in the southern boreal zone would be strongly associated with climate. We predicted that the biomass of coniferous trees would increase with increasing wetness and colder temperatures, while poplars and birch would increase in biomass with temperature and dryness. We expected that all songbird groups would be more constrained by non-climate factors, thus the “resource hypothesis” would be more supported in general. However, we recognise that both “physiology” and “resource” could be limiting factors and equally plausible hypothesis for some groups. Moreover, the direct influence of climate can also indicate unmeasured factors that are not necessarily related to physiology but to resources instead, such as food availability. Recognizing this limitation, we expected that coniferous-associated species would be constrained by their physiology to some extent and thus more influenced by climate directly (“physiology hypothesis” supported) given that they are climatically vulnerable based on their boreal-restricted distribution. Meanwhile, deciduous-associated species would be more constrained by vegetation composition and structure and more influenced by the indirect effects of climate as well as other non-climate factors (i.e., more support to the “resource hypothesis”). We also hypothesized that wetland-associated species would be more driven by resources given the lack of terrain diversity in wetlands, which could suggest a more homogenous climate (“resource hypothesis” supported). We predicted that birds associated with coniferous environments would be more influenced by the biomass of specific tree species, particularly white and black spruce. Moreover, birds that are more associated with wetlands would respond positively to black spruce.

Methods

Study area

We used occurrence data from surveys for passerine birds (hereafter, songbirds) across the province of Alberta, Canada. The study area encompasses a range of habitat types across a latitudinal gradient in boreal forest, parkland, and grassland ecoregions, including local elevation and topographic differences (Figure 3.1). The parkland ecoregion is a transition zone between the grasslands in the south and boreal ecoregions in the north and consists of an aspen and grassland mosaic interspersed with occasional balsam poplar (*Populus balsamifera*) and white spruce in wetter and cooler microclimates. We supplemented existing data from the Alberta Biodiversity Monitoring Institute (http://www.abmi.ca) with additional surveys in areas with more terrain variability (i.e., river valleys and hill systems. We avoided the Rocky Mountains because they are wetter and less seasonal than boreal environments, and contain different floristic communities. Vegetation in the boreal plains and northerly sites were a mix of peatlands, dominated by black spruce and upland mixedwood forest containing a mix of coniferous tree species, primarily white spruce, and deciduous species, chiefly birch (*Betula* spp.), trembling aspen and balsam poplar (*P. balsamifera*). River valleys of southern Alberta, where grasslands predominate, included treeless slopes and Plains cottonwood (*P. deltoides*) in valley bottoms. Farther north near the parkland transition zone (~52° N), trees are distributed along both valley bottoms and slopes with lower sun exposure. Hills systems are rare in the southernmost part of the province except for Cypress Hills, a relict of white spruce and lodgepole pine within a prairie system (Moss, 1955). Higher elevation and incised valleys are the main drivers sustaining coniferous trees in that area (Moss, 1955). Cypress Hills and other hill systems farther north are the result of differential fluvial erosion of sedimentary bedrock during the Quaternary glaciations, which resulted in hills and valleys formations that tend to be cooler than adjacent flat areas (Dyke 2012).

Summer temperature and associated evapotranspiration limit the southern distribution of boreal forests (Hogg, 1994). At colder and wetter sites in the north, such as in the lower and upper boreal highlands (57° N through 59° N), mean annual temperatures can range from -5 to 0.8 °C (30-year normal; 1961 – 1990), and precipitation ranges from 375 – 582 mm per year. Along the dry mixed wood forests of northwest, such as along the Peace River region (54.7° N through 58° N), and in central Alberta (51.7° N through 54.9° N), conditions are warmer, and temperatures range from -2 – 3 °C with similar precipitation levels 376 – 597 mm per year. The central and southern regions (49° N through 55° N) experience long dry and hot periods during summer and warmer temperatures during winter. For instance, in the central parkland, mean annual temperatures range from 1.4 – 3.6 °C and precipitation from 373 to 536 mm, while grasslands temperatures range from 2 – 5.8 °C, with precipitation between 260 – 394 mm (Downing and Pettapiece, 2006). As temperatures and precipitation increase further west, grasslands, mixedwood and parkland ecoregions in proximity to the Canadian Rocky Mountains are warmer and wetter.

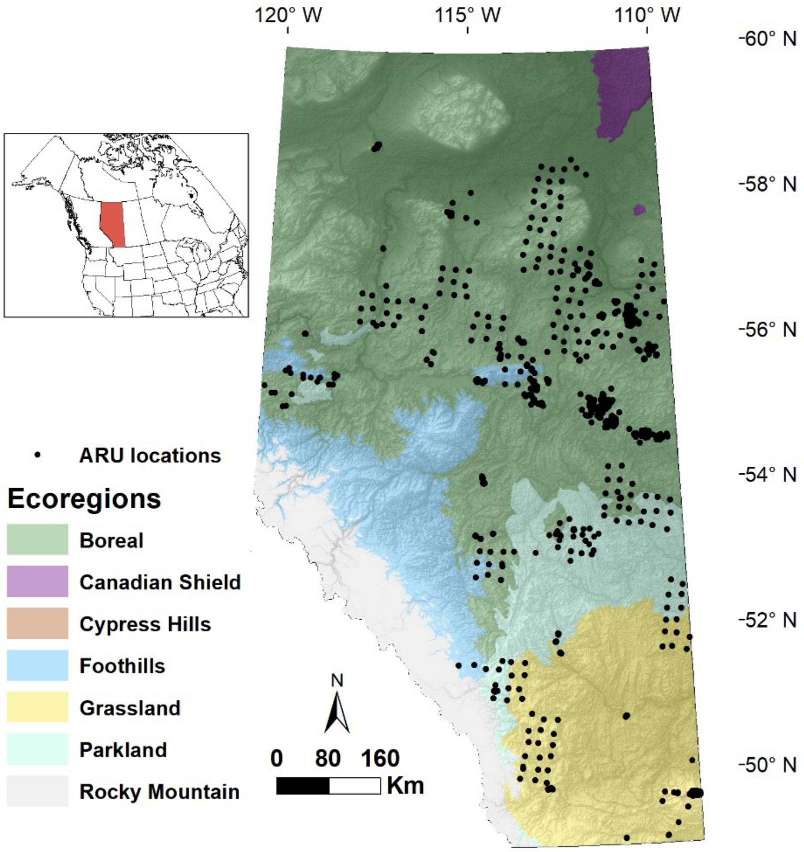

Figure 3.1: Location of acoustic recording units (ARUs) across Alberta, Canada. Ecoregions are shown overlaid over a hill shade depicting the gentle topography across the region.

Songbird sampling

We used sensor data collected by the authors and by the Alberta Biodiversity Monitoring Institute, accessed via the WildTrax sensor data repository (https://wildtrax.ca). Data were collected between early spring (mid-May) and early summer (mid-July) between 2012 and 2018 (ARUs; Shonfield and Bayne 2017). We had >300 m between ARUs and sampled locations, which had <50 % of human disturbance in a 300 m buffer to minimize the effects of land use on bird occurrence. We set ARUs (N=2147) to record for 3 min at a pre-determined schedule from sunrise to late morning. We processed recordings and identified songbirds by sound while prioritizing recordings made near sunrise. During adverse weather events that could impair bird identification, we listened to recordings later or on a different day until we reached four recordings from each location.

We built encounter histories for use in occupancy models (see details below) for each species based on the history of detections at each location by assigning presences (1) or absences (0) for each recording. We focused our analysis on forest and wetland specialist species, where >50% of their population is estimated to breed in the boreal forest (i.e., *boreal songbirds*), based on information from the Boreal Songbird Initiative (https://www.borealbirds.org), and where our models converged, which led to a final number 16 of out of 87 species detected ($N_{\text{Coniferous}} = 9$; $N_{\text{Deciduous}} = 3$; $N_{\text{Wetlands}} = 4$). We classified these species into three different groups according to their nest habitat preferences, which were “Coniferous-associated”, “Deciduous-associated”, and “Wetland-associated” species.

Environmental variables

For each ARU location, we extracted a suite of environmental variables that fit into five broad categories: climate, vegetation, forest structure, and soil characteristics. Table 3.1 summarizes the variables used in this study.

Climate: We included macroclimate data from the 30-year normal period of 1961 – 1990 for Alberta using ClimateNA, a standalone software that derives bioclimatic variables from PRISM (Daly *et al.*, 2008) at a scale-free resolution (Wang et al., 2016 and details within). We supplied a 100-m DEM to the software to extract annual climate metrics. We generated spatially explicit estimates of summer (June, July, and August) climate moisture index (CMI), May to September precipitation (MSP), growing degree days above 5 ˚C (GDD>5), and mean minimum winter temperature (Tmin). Following the models and procedures developed by Estevo et al. (2022), we downscaled CMI and Tmin predictions from ClimateNA to incorporate topographic effects at the local level using a modified approach from Holden et al. (2016). This method involved correlating *in-situ* climate measurements sampled with data loggers (Thermochron iButton model DS1922L) to develop temperature offsets, which are then combined with climate grids available at larger scales to incorporate small-scale forcing factors (e.g., Holden *et al.*, 2016). We used temperature data aggregated monthly from iButton dataloggers deployed between 2014 and 2020 in river valleys and hills systems (N=283) in Alberta to generate offsets of maximum, mean and minimum temperature. To do this, we first extracted monthly maximum, mean, and minimum temperatures from ClimateNA to the same locations and years iButtons were deployed. We then calculated the difference between iButton and ClimateNA prediction for each temperature metric and then modelled the difference as a function of the suite of topographic derived variables and tree cover (Estevo et al., 2022). The topographic variables included the topographic position index (TPI), topographic roughness (TRI), heatload index (SolRad), and the compound topographic index (CTI). All topography variables were calculated from a 50-m digital elevation model (DEM) derived from 1:50,000 Topographic Data of Canada (CanVec series). We derived tree cover data from the spatial landcover inventory layer developed by the Alberta Biodiversity Monitoring Institute ('Wall-to-wall Land Cover Map' version1.0 from 2010 retrieved from http://www.abmi.ca, ABMI, 2010), which included coniferous, broadleaf, and mixedwood cover types. We then created spatial predictions of these offsets and added them to their corresponding variable for the normal periods to generate adjusted climate variables.

Vegetation: We used model-based maps of Canada's forest attributes based on the Canadian National Forest Inventory (Beaudoin et al., 2018) to extract the relative biomass (%) of white spruce, black spruce, poplars (aspen, balsam poplar, plains cottonwood, and narrow-leaved cottonwood, *Populus angustifolia*), and birch.

Forest structure: Using National Forest Inventory vegetation maps (Beaudoin et al., 2018), we extracted the age (years) of the leading species and crown closure (%) at each ARU station. We also used the time series of images from the Sentinel-2 satellite (Gascon et al. 2014) to calculate the normalized differential vegetation index (NDVI) for the boreal summer period (June, July, and August) from 2012 – 2018 as a proxy of overall forest productivity. We filtered the image collection for pixels that contained < 30% of granule-specific clouds taken from the original metadata, and then made composite maps for each year using the median of each pixel and calculated NDVI for that year. We then averaged the six-year periods of NDVI to generate a single NDVI image for Alberta. These procedures were conducted in the Google Earth Engine geospatial processing service (Gorelick *et al*. 2017*)*. We also calculated a measure for forest patch area for each ARU location using canopy cover data from the 'Wall-to-wall Land Cover' product (ABMI, 2010). We grouped polygons of broadleaf, conifer and mixedwood forests from the land cover map and rasterized it to a 50-m resolution to generate a binary layer of presence/absence of forests. Then, we used the *landscapemetrics* package (Hesselbarth et al., 2019) in R environment (R Core Team, 2013) to define individual patches of forest. We used the function *window_lsm* and calculated the average patch area for a focal cell in a neighbourhood of 21 x 21 pixels (approx. 2 x 2 km). Finally, we extracted wetland probability for each ARU station from the Boreal Wetland probability dataset developed by the Alberta Biodiversity Monitoring Institute (Hird et al., 2017).

Soil properties: we extracted soil characteristics to model plant abundance using the Soil Landscapes of Canada database (version 3.2, Schut et al., 2011). We extracted estimates of the percentage of sand and clay from rasterized polygons at 100 m resolution.

Our goal in incorporating forest structure and soils was to control for their effects on vegetation and songbird occurrence. Despite the importance of those variables, we focused our results and discussion on the effects of climate, vegetation and composition.

Based on nesting habitat and life history, our expectation for each functional group was that they would respond to variables most associated with their respective nesting habitat (e.g., coniferous-associated species being positively impacted by spruce trees).

Table 3.1: Abbreviation and definitions of environmental variables used in the modelling.

Category		Variable	Units	Definition
Topography		TPI	-	Topographic position index calculated at a circular radius of 300 m
		TRI	-	Terrain roughness index
		SolRad	MJ/cm2/year	Heatload index
		CTI	-	Compound topographic index
Tree composition		Poplars	%	Relative biomass of poplars (Populus spp.)
		Birch	%	Relative biomass of birch (Betula spp.)
		Wspruce	%	Relative biomass of white spruce (*Picea glauca*)
		Bspruce	%	Relative biomass of black spruce (*P. mariana*)
Climate	**Macroclimate**	DD5	-	Growing Degree Days
		MSP	mm	May to September precipitation
	Adjusted Climate	CMI	-	Summer climate moisture index
		Tmin	mm	Mean minimum winter temperature
Vegetation structure		Age	years	Age of leading species
		NDVI	-	Normalized difference vegetation index
		PAr	ha	Average patch area within a 21 x 21 window
		Wetprob	%	Wetland probability
		Cclosure	%	Crown closure
Soil characteristics		tclay	%	Percentage of clay in the soil
		tsand	%	Percentage of sand in the soil

Statistical Analysis

Occupancy models

We estimated the occupancy of individual songbirds at each location using single-species occupancy models (Mackenzie et al., 2005). This approach estimates the probability that the species will be present at each location at some time during the survey season by accounting for imperfect detection related to bird movement and singing behavior. Our first step was to build a null occupancy model for each individual species that accounted for the time of the recording, Julian date and the amount of forest (%) around each ARU station to account for differential sound attenuation in various vegetation types. We derived percent forest with the same categories from the wall-to-wall mapping tool from the Alberta Biodiversity Monitoring Institute (see *Forest structure* above) by considering coniferous, broadleaf and mixedwood forests at a 50-m resolution and then calculating forest cover in a 300-m buffer around each ARU station. Next, we extracted the posterior estimates of occupancy probability for each species and calculated the conditional probabilities of occurrence based on the suite of detection variables. We used the *unmarked* package (Fiske and Chandler, 2011) in R (R Core Team, 2013) to build null occupancy models.

Piecewise Structural Equation Modelling

We used the posterior estimates of occupancy probability from the previous step as response variables when building piecewise structural equation models (pSEM). Different from typical SEMs, pSEMs allows one to analyse directed multivariate path models in a generalized context, while fitting models with different statistical distributions (Lefcheck, 2016; Shipley, 2009). Our first approach was to model the species-level occurrence of birds and relative tree biomass by fitting occurrence and relative biomass with a beta distribution. For that, we transformed occurrence probability estimates, as well as relative biomass of trees, by compressing the range of values to avoid zeroes and ones using the Smithson and Verkuilen (2006) method as follows:

$$\psi^{*} = \frac{\psi(n-1) + 0.5}{n}$$

Where ψ^{*} is the transformed occupancy estimate ψ (or relative abundance of trees), and n is the sample size.

We built models of bird occurrence as a function of the additive and direct effects of relative biomass of trees, climate and forest structure. Table 3.1 shows the variables in each category. Climate variables included macroclimate (MSP and DD5) and locally adjusted climate (CMI), except T_{min} which we only allowed to have direct effects on plant biomass. Simultaneously, we modeled the relative biomass of each tree species as a function of soil characteristics and climate (both macroclimate - MSP and GDD5; and locally adjusted climate - T_{min} and CMI). We did not include topography variables in our modelling as these variables were part of our locally adjusted climate variables. T_{min} was only included as a direct effect on the relative biomass of trees and therefore only had an indirect effect on bird occurrence. Figure 3.2 shows a scheme of our modelling approach.

We fit individual models (i.e., structural equations) with generalized linear mixed models using the *glmmTMB* package in R (Brooks et al., 2017) and then fitted pSEMs with the *psem* function within the *piecewiseSEM* package (Lefcheck, 2016). We ran the same models from the previous step with the *betareg* function within the *betareg* package (Cribari-Neto and Zeileis, 2010) to estimate direct and indirect effects, as well as mediator variables, and associated 95% confidence intervals, based on 10,000 bootstrapped iterations with the *semEff* function in the *semEff* package (Murphy, 2020). Mediators are variables that influence the process through which two or more variables are related as they stand in between a predictor and response variable. Independent variables can have a direct and indirect effect on response variables when a mediator is involved (Fan *et al.*, 2016). *semEff* calculates mediators as the sum of all the indirect paths from all predictors which involve each mediator and provide an overall importance and net direction for its effect (Fan *et al.*, 2016). Therefore, the estimates for the indirect effects refer to the net indirect effect of a given climate variable through all tree composition variables (the mediators). Then, mediator estimates refer to the summary of all indirect effects that involve a given mediator, provide a sense of which mediator is most important, and provide the net direction of all indirect effects together. We calculated semi-partial correlation coefficients (hereafter β coefficients) to adjust for multicollinearity among predictors by dividing by the square root of variance inflation factors, which allowed us to build path graphs that fully partition effects within species pSEMs (Murphy, 2020). Therefore, βs indicate the change in standard deviations (SD) of the response variable per change of one SD in a predictor variable; they indicate individual contributions of a given variable to the multiple regression coefficient, where coefficients are bound to $-1 \leq \beta \leq 1$ (Murphy, 2020; Nayebi, 2020). We evaluated overall model fit by performing tests of directed separation (*d-sep*) between variables that did not have a path between them in our model. Tests of directed separation determine the dependence or independence of variables after statistically holding constant other variables (Shipley, 2009), therefore testing if claims about a variable are truly independent. *d-sep* tests can then be summarized to a C statistic that combines all probabilities (p) of unspecified paths in a single score, which can then be compared to a chi-square distribution (Shipley, 2009). Therefore, the hypothesized relationships in a graph are consistent with the data if there is weak support for *C* (the sum of all conditional independence claims), in which case *p* for chi-square test is > 0.05. In addition, we evaluated variance explained (pseudo-R^2) of individual pSEMs. By following these steps, we only included individual species pSEMs for which the probability of the *C* statistics was not significant (i.e., $p > 0.05$), indicating that the paths weregenerated by causal processes. We averaged path coefficients by bird nesting habitat group to graph effects on species occurrence and make inferences about direct, indirect, and mediator effects.

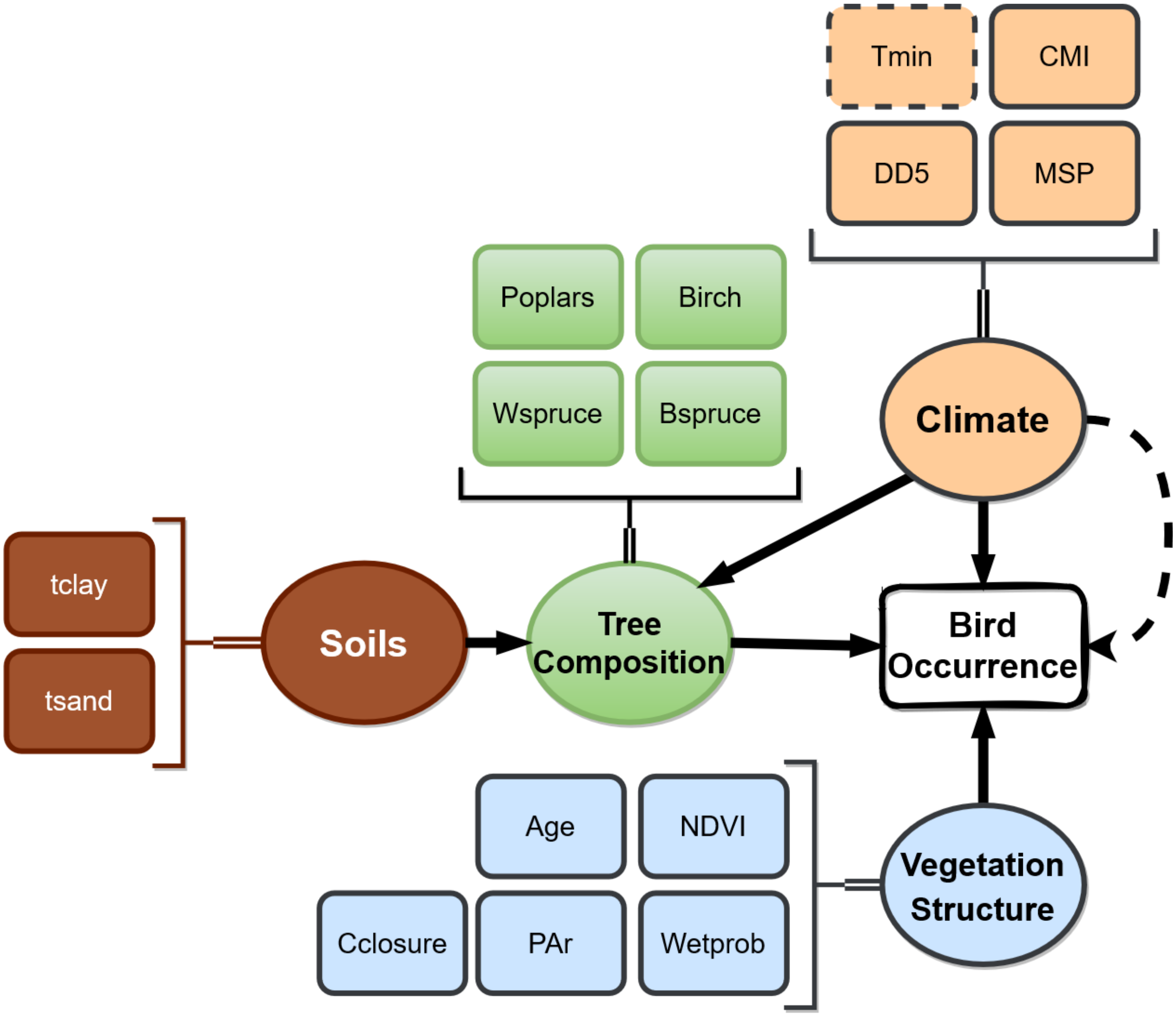

Figure 3.2: Conceptual structural equation model for the effects of vegetation, climate, and habitat structure on the occurrence of boreal songbirds. Solid arrows

indicate direct effects, while dashed lines indicate indirect effects from climate variables on songbird occurrence via vegetation. All climate variables have direct effects on songbirds, except Tmin (dashed square). Indirect effects of soils have been omitted. Refer to Table 3.1 for variable abbreviations.

Results

Effects of climate and soil characteristics on tree biomass

Bootstrapped semi-partial correlation coefficients indicated that all variables had significant impacts on vegetation, except for total sand in relation to white spruce and birch (Figure 3.3). Poplars increased with MSP. Effects of all climate variables were smaller on white spruce, relative to other tree species and groups. Birches were most affected by CMI. CMI and GDD5 were the strongest (positive) predictors for trees, particularly for black spruce, where the effect of CMI was 3-4 times larger than the effect of MSP. While the direction of impact changed between variables depending on the tree species in questions, T_{min} was consistently negative.

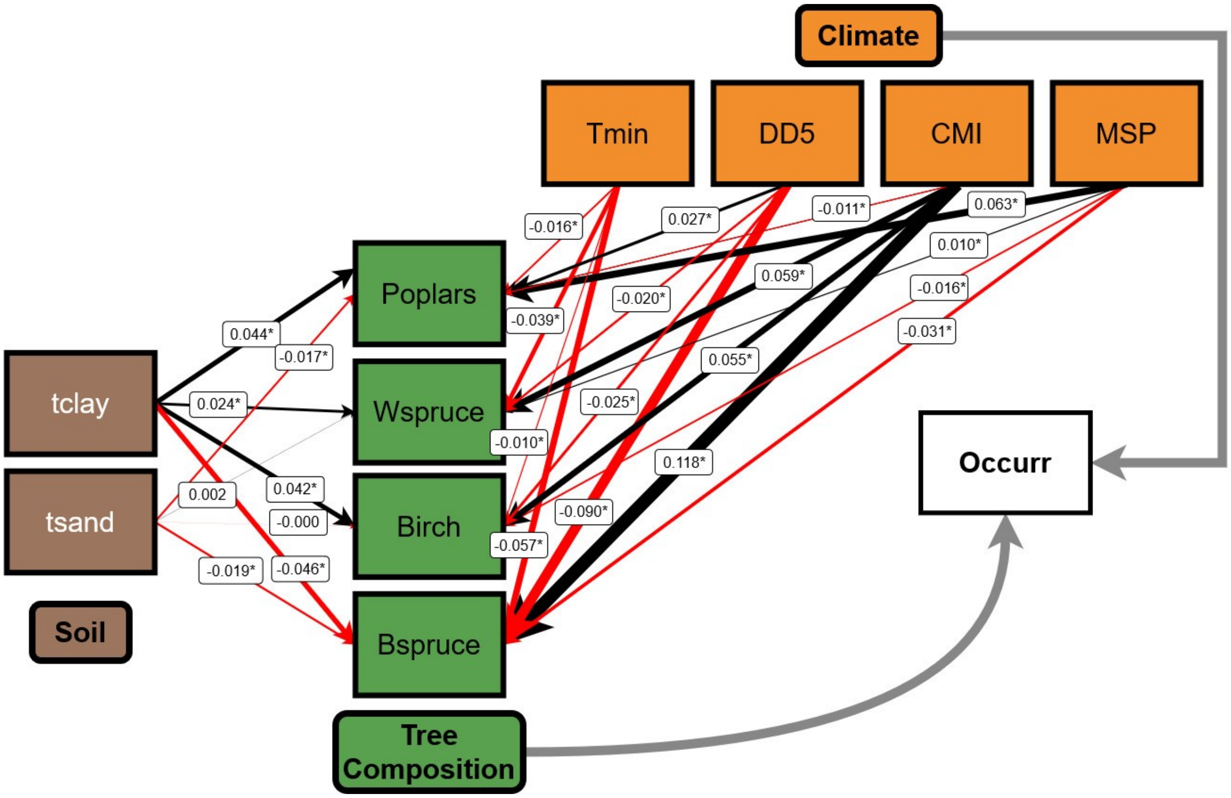

Figure 3.3: Effects of climate and soil variables on different tree species or groups' biomass. Red/black arrows denote negative/positive effects of a given variable

on each species. Line thickness is proportional to the effect size (numbers in boxes). '*' indicates significant effects. Effects of climate and vegetation on songbird occurrence (Occurr) have been omitted in this figure for clarity. Refer to Table 3.1 for variable abbreviations.

Effects of climate, tree composition, and forest structure on songbirds

Direct and indirect effects

The direct strength of influence of climate, vegetation composition, and vegetation structure varied across bird groups (Figure 3.4 and Figure 3.5, Table S3.1). In general, coniferous-associated bird species were most strongly affected by tree composition and vegetation structure, particularly black and white spruce (both positive), but also strongly impacted by climate (DD5 and CMI). Though the signal (positive or negative) of the effects of a given variable was generally consistent between the different variable types, effects for vegetation structured varied slightly more for coniferous-associated species. For example, patch size had a positive effect on Blue-headed Vireo (*Vireo solitarius*, β = 0.007), Yellow-rumped Warbler (*Setophaga coronata*, β = 0.009) and Boreal Chickadee (*Poecile hudsonicus*, β = 0.023), but negative for the other species, particularly for Blackpoll Warbler (*Setophaga striata*, β = -0.048), White-winged Crossbill (*Loxia leucoptera,* β = -0.042), and Golden-crowned Kinglet (*Regulus satrapa*, β = -0.032) (Table S3.1). We observed that tree composition, especially spruce biomass, had a stronger and negative effect on deciduous-associated songbirds (Figure 3.5), followed by vegetation structure (NDVI and crown closure), while climate had small impact on their occurrence. Wetland-associated species were most strongly influenced by climate (DD5 and CMI in particular), and vegetation structured (crown closure).

The strength of indirect effects of climate variables, via their impacts on trees, was similar to their direct counterpart in some cases, but were weaker overall. For example, the direct impacts of CMI on coniferous- and wetland-associated songbirds was 5 – 16 times stronger than its indirect impact (Figure 3.4, Table S3.1). Meanwhile, CMI and MSP, to a minor extent, had the same impact both directly and indirectly on deciduous-associated species. By summing the absolute total effects (the sum of all direct and indirect effects of a given variable) across variable types and species within a nesting habitat group, we observed that tree species composition and forest structure were 0.8 – 2.5 times stronger than climate for coniferous-associated species and deciduous associated species. For wetland-associated species, climate was 1.3 – 2.4 times stronger than tree composition or vegetation structure (Figure 3.5, Table S3.1).

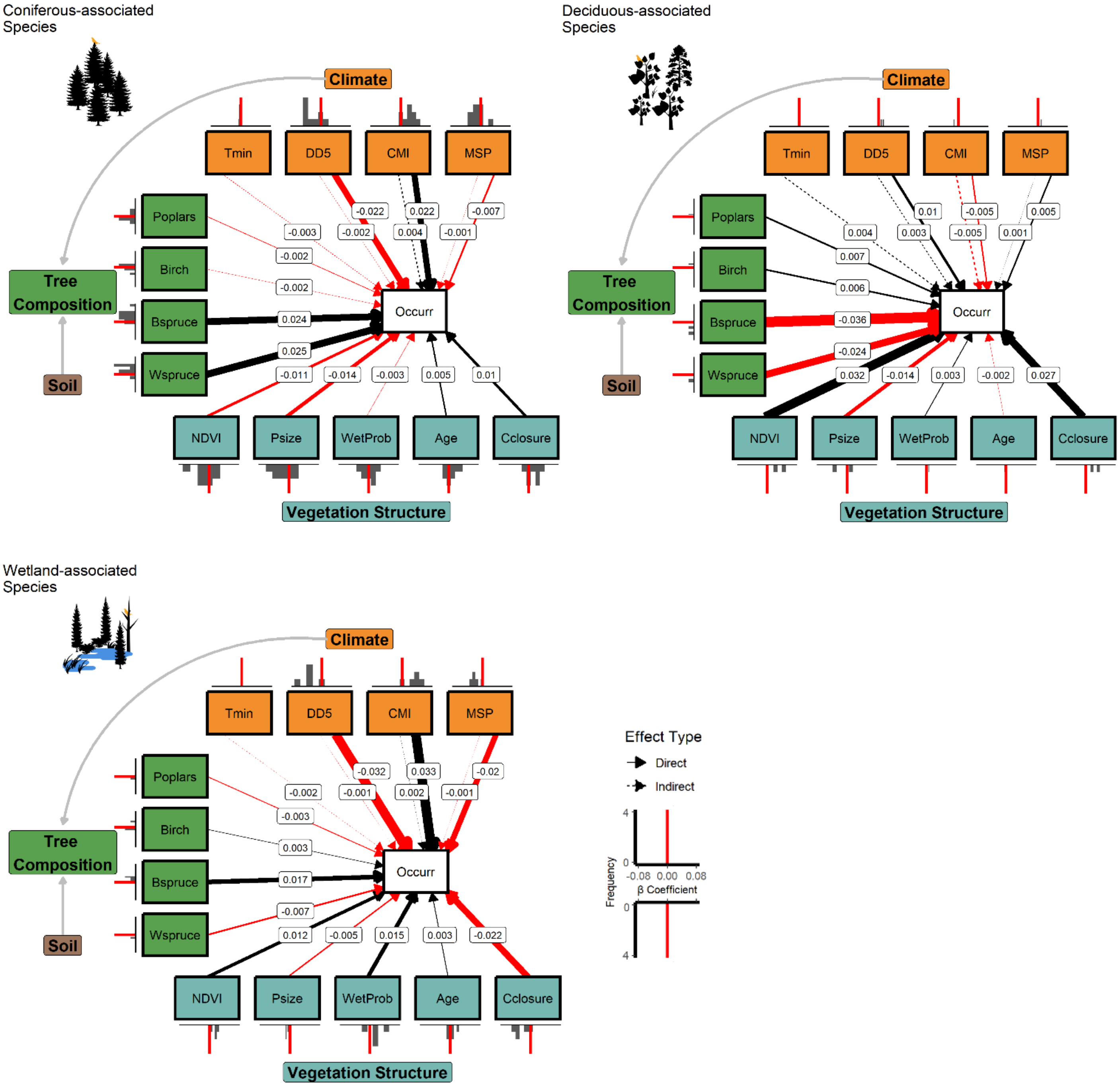

Figure 3.4: Direct and indirect effects of climate, tree composition and vegetation structure on boreal songbird occurrence in Alberta, Canada. Arrows are colored according to the direction of the effect, either positive (black) or negative (red), and their

width are proportional to the effect size (numbers in boxes). Refer to Figure 3.3 for the effects of climate and soil on vegetation (omitted in this figure). Bar graphs on top of each variable represent the frequency distribution of the effect (β coefficients) of that variable across species within a particular group, where the line in red marks zero. Refer to Table 3.1 for variable abbreviations.

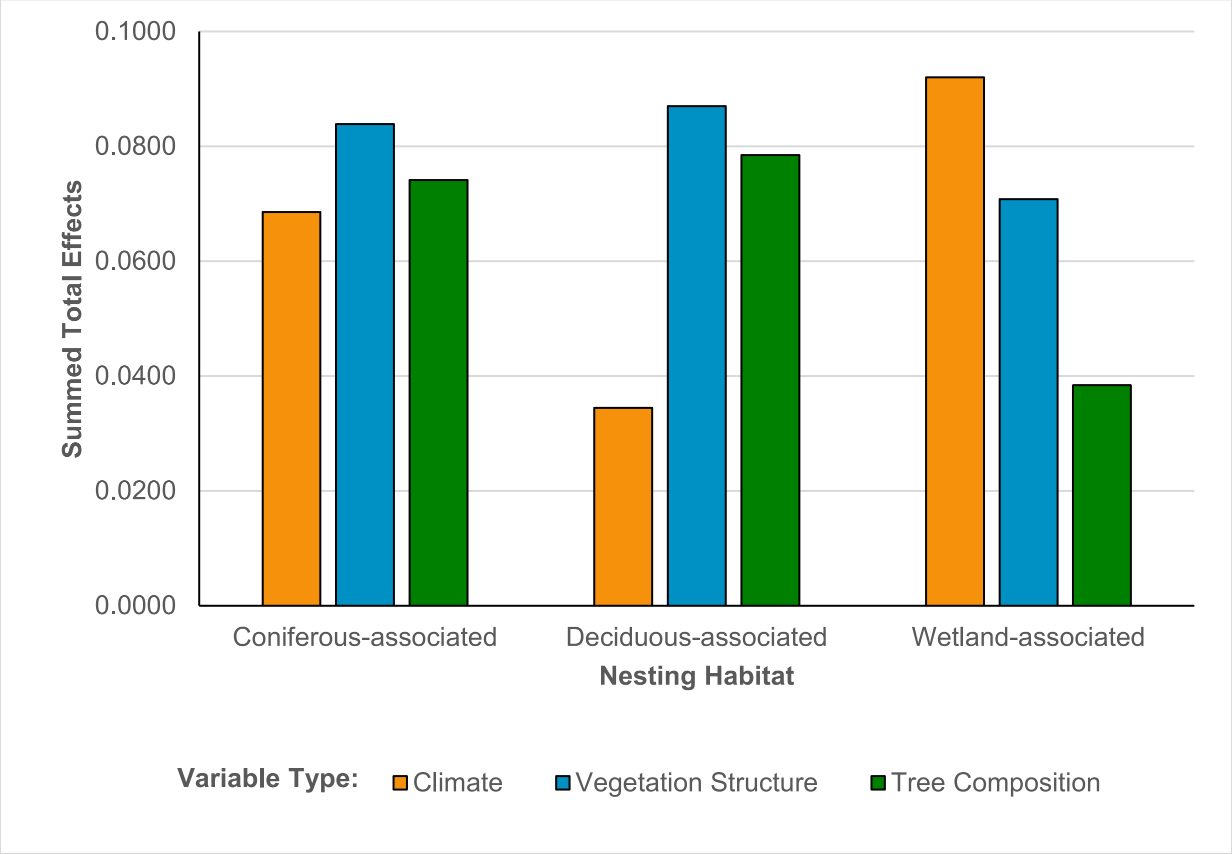

Figure 3.5: Summed total effect of climate, tree composition and vegetation structure variables per nesting habitat of boreal songbirds in Alberta, Canada. The total effect (β coefficient) of each variable within each variable type category were summed per species and then summed across nesting habitat groups. Refer to Table S3.1 for species-specific coefficients.

Mediators

Indirect impacts were mediated disproportionally between the different tree species/groups analyzed but were much weaker than direct effects (Figure 3.6). The relative biomass of spruce species was by far the most important mediators of the indirect effects of climate, both in strength and by the number of species in which effects were significant. Overall, the indirect effects of climate were more strongly mediated through black spruce (mostly negatively) and white spruce (mostly positive). This result indicates that the net direction of all indirect impacts of climate on coniferous- and wetland-associated birds was in general negative via black spruce and positive through white spruce (for coniferous-associated birds only). Mediation of climate through black spruce was strongly positive for deciduous-associated species. Birch and poplar mediation effects were much smaller in strength, but mediation through poplars was significant for as many species as white spruce.

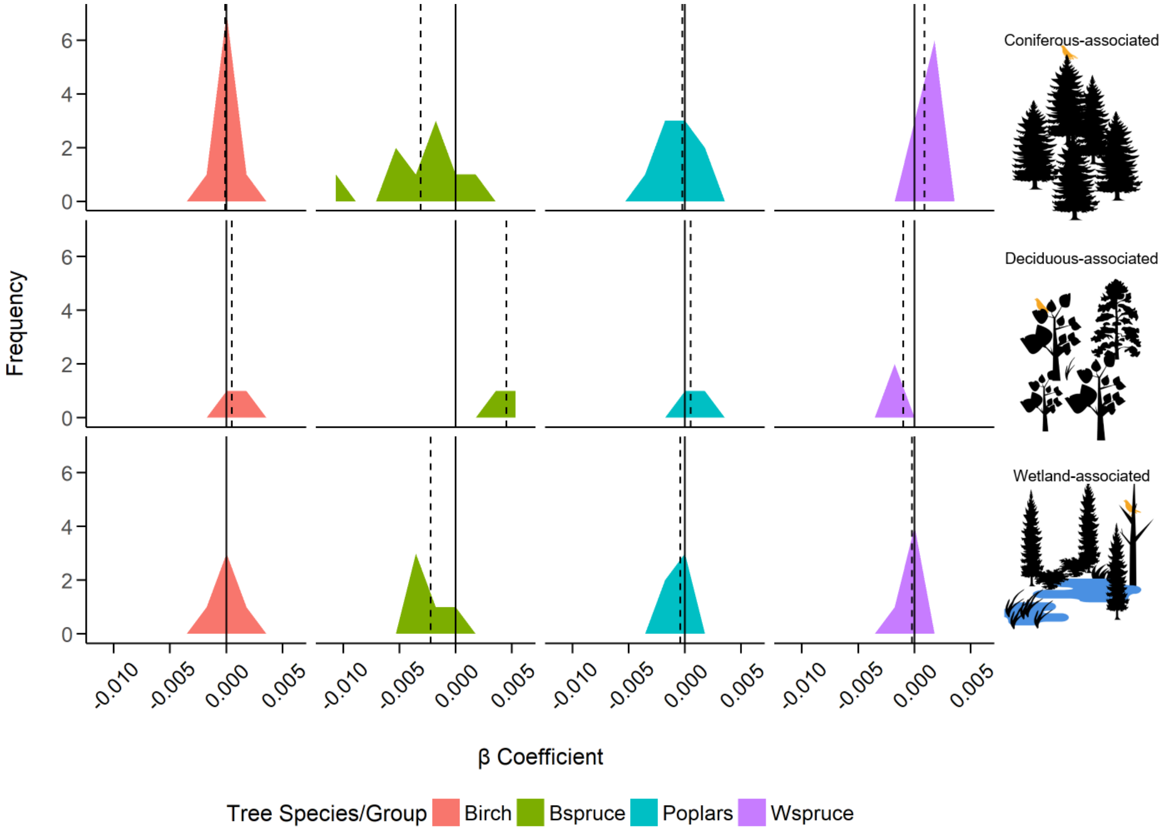

Figure 3.6: Mediating effects of different tree species/groups on boreal songbirds. Solid vertical lines indicate zero, while dashed lines indicate the mean mediator effect of the tree species for a given group. Bspruce – black spruce; Wspruce – white spruce.

Discussion

We disentangled the direct and indirect effects of climate and vegetation on several boreal-breeding songbirds across a climate gradient in Alberta, Canada. Overall, our results indicate the direct effects of climate were substantially stronger than its indirect effects for coniferous- and wetland-associated species, but for deciduous-associated species the indirect impacts were sometimes comparable in strength with other direct climate factors. Tree composition and vegetation structure were stronger drivers than climate for both coniferous- and deciduous-associated species. Climate had substantially stronger impacts than tree composition or vegetation structure for wetland-associated species.

Effects of climate on vegetation

Climate is a major driver of the distribution of trees in western boreal forests, wherein boreal trees are adapted to cold temperatures, and short growing seasons. At the regional level, the distribution of the major tree species we modelled is understood to be determined by their sensitivity to moisture balance and limited by hot-dry conditions (Hogg 1994). The effects of climate on the biomass of trees in our models corroborate this general understanding of constraints on western boreal trees, in that the relative biomass of white spruce and black spruce increased with more available moisture and cooler temperatures (i.e., increasing climate moisture index, CMI; Hogg 1994), particularly for black spruce. Our results also highlighted that the temperatures experienced over winter at the local level (i.e., adjusted T_{min}) had negative effects on the relative biomass of all tree species and groups analysed. The impacts were particularly strong for spruce species, which suggests that their growth and overall health may still be limited by winter minimum temperatures (Rossi and Bousquet, 2014; Harrington and Gould, 2015). Winter temperatures are an important physiological marker for spruce and required for dormancy (Harrington and Gould, 2015). Similar results regarding winter minima limiting the distribution and growth of boreal trees have also been found at broader scales (McKenney and Pedlar, 2003; Griesbauer and Green, 2012; Stralberg *et al.*, 2018). Following a similar pattern, growing degree days (DD5) also had negative impacts on most trees, except for poplars, suggesting that the accumulation of heat (or forcing units) in boreal trees may inhibit their growth or productivity to some extent. Growing degree days can have negative impacts on plant growth in other parts of Canada (Searls *et al.*, 2021), which has been associated with temperature-induced stress in areas with cold and dry conditions, which comprise most of the boreal plains region (Barber, Juday and Finney, 2000). Although that could be the case here, tree responses to the accumulation of heat varies spatially, particularly through latitude, such that northern populations respond more positively to heat accumulation (Lapointe-Garant *et al.*, 2010). We did not explore that spatial difference, but our results may suggest that in general the biomass of trees at the southern edge of the boreal plains is under heat stress, in that heat and its effect on moisture availability does limit the establishment of trees. Moreover, this result may be because boreal trees perform a trade-off between chilling exposure and accumulation of heat for bud burst (Harrington and Gould, 2015), and as cold adapted genotypes, in general, boreal trees are triggered by cold periods to enter dormancy and may require less heat for bud burst and growth during cold periods.

Direct effects of tree composition and forest structure on songbird occurrence

Direct effects of tree composition followed most of our expectations, where songbirds in each nesting habitat group responded more strongly to tree species typifying their habitat associations. Our results show that coniferous trees, such as white spruce, had higher impact on the occurrence of coniferous-associated birds, but the opposite effect for deciduous associated songbirds. Accordingly, wetland-associated species occurred more frequently with higher biomass of black spruce, which is a common tree in bogs and other wet areas in the boreal forest. We see these results as reassuring that our models are capturing most of the expected effects from tree composition for a given nesting bird group.

The results for forest structure also corroborated our expectations based on life history (i.e., species nesting habitat association). The occurrence of songbirds associated with both coniferous and deciduous forest increased with crown closure, which can be traced to how canopy closure can be an indication of structural complexity and cooler microclimates (Frey et al., 2016), which may explain the positive impact on deciduous- and coniferous-associated songbirds. Patch size had a consistent negative impact on songbird groups, which may be related to density dependence in patchy landscapes. For instance, density and abundance of forest birds may decrease with patch size (*i.e.* negative effect; Lee *et al.*, 2002). However, the signal (positive or negative) varied considerably across species within the same group, particularly for coniferous-associated species, which may reflect that for some species density may be higher in patchy landscapes because habitat is more limiting. Even though we surveyed recent boreal refugia analogs in the central portion of Alberta that contain some similarity in terms of tree composition and local cooler climate (Estevo *et al.*, 2022), these patches are still considerably small and isolated. Wetland probability had an expected positive impact on wetland-associated species. The negative effect of wetlands on conifer-associated species may reflect their mostly upland affinities. Finally, vegetation greenness was indicative of high occurrence of songbirds across all groups, corroborating to the hypothesis that more productive forests can sustain more species and increase local occurrence (Goetz *et al.*, 2007; Cumming *et al.*, 2014).

Direct and indirect impacts of climate and mediator vegetation on songbirds

Climate influences on songbird occurrence and availability of their habitat represent a conundrum in ecology. Both plants and wildlife are directly affected by climate, but wildlife may also be affected by the impacts of climate on plants (indirect effects). Climate has generally been the primary factor used to describe the broad scale distribution of songbirds; tree composition and forest structure are usually incorporated only at finer scales, making the indirect effects of climate vastly underestimated. Here we provide insight on how much these indirect effects play in species occurrence for three different boreal songbird groups. Our results indicate that overall deciduous-, wetland- and coniferous-associated species are more limited by climate directly than indirectly, because the direct impacts of climate were much bigger than the indirect effects (1 to 32 times). However, climate was more influential than tree composition and vegetation structure to wetland-associated species only (1.3 – 2.4), suggesting more support for the physiology hypothesis for this group and the resource hypothesis for the coniferous- and deciduous-associated species. For example, factors such as growing degree days, one of the strongest climate predictors of occurrence for conifer and wetland birds, may affect birds directly by negatively impacting their reproductive success (Telenský *et al.*, 2020), while precipitation may have similar effects. However, direct climate impacts on physiology are stronger under extreme circumstances, such in cases with extreme weather events (Hawkins et al., 2003; McCain, 2007, 2009; McKechnie & Wolf, 2010; Buckley et al., 2012). For example, extreme heat waves can lead to mass mortality of individuals, even in the presence of nearby water (Wingfield *et al.*, 2017), which is a clear example of the direct climate impact on birds' physiology. Though it is possible that such events could have happened during the span of this study, it is unlikely that the strength of direct climate capture here on wetland- and coniferous-associated may be purely a function of climate impacts on songbird physiology. Furthermore, most of the species detected probably have a wide climate plasticity because of their migratory behaviour and experience a wide range of climate conditions throughout their life history. Climate plasticity suggests that there might be unmeasured vegetation variables, unaccounted impacts of climate on vegetation structure and resources, and interspecific interactions at play. Therefore, suggesting more support for the physiology hypothesis for wetland-associated may not necessarily be precise, the strong impacts of climate could well be the impacts of climate on resources (i.e., resource hypothesis supported). Climate and moisture have a direct positive connection with the limits of the boreal biome, where vegetation zones typical of western boreal forests are in equilibrium with moisture (Hogg, 1994). However, we found that the effect of climatic moisture balance on measured vegetation variables was small, which may indicate a mismatch between the particular climate and vegetation variables examined. Therefore, the effects of climate moisture might best be observed in different vegetation variables than those examined here. We also found that taking all individual species responses by variable type (climate, tree species composition, and vegetation structure), the impacts of tree composition were stronger than climate or structure for deciduous- and coniferous-associated species, while climate had an average stronger effect for wetland-associated species (e.g., Figure 3.5). However, the variation in directionality and strength of these effects within the same group (and even within the same variable) may indicate that comparing different variable types may be misleading and omits important information about key variables. For instance, growing degree days and CMI were clearly important variables for coniferous-associated species and comparable in strength with white and black spruce effects, but their strength was diluted when we examined at the average climate impact. In addition, nesting habitat groups were disproportionally represented, such that taking average effects from only a couple of deciduous-associated species may not necessarily provide a comprehensive understanding for a group with a range of life histories and distributions.

It is important to consider the impact that vegetation had in mediating the impacts of climate on songbirds. Even though the absolute strength of this effect was generally low, spruce trees exhibited stronger mediating effects than other tree species, suggesting that spruces are important not only in terms of their direct impact on songbirds (e.g., nesting habitat), but also as a climate filtering mechanism for species. A variety of plant attributes respond directly to climate, which then affects different aspects of the wildlife that rely on them. There are numerous examples that stem from trophic relationships. For instance, warm temperatures and high levels of precipitation may generally lead to higher production of food resources for animals (Jetz *et al.*, 2008). Usually though, the existing evidence comes from fast responding biomes, such as tropical forests, where tree growth, food production, respond to climate at short temporal scales. Given the slow growth of trees in the boreal biome, it can be expected that trees mediate climate impacts on songbirds through long temporal scales, which in turn translates as relatively weak effects on bird occurrence. The evidence of slow climatic shifts of boreal trees, which are followed by range shifts of wildlife (D'Orangeville *et al.*, 2023), is likely evidence of the mediation impact that trees may have. The lagged response of vegetation to climate may also explain why climate was a stronger predictor than vegetation in some cases.

Implications and limitations

It is important to consider the implications of these results in the context of a warming climate. Climate at broad scales is a major limiting factor delineating species range, as well as the main predictor of areas that are relatively resistant to climate change (i.e., refugia; Albright et al. 2017, Stralberg 2018). However, we found that climate, vegetation and forest structure may be similarly important factors defining the occurrence of boreal songbirds at finer scales. Notably, tree composition and habitat structure will be affected by a changing climate and will consequently affect songbirds. Our results suggest that climate change impacts on birds will extend beyond the effects in their physiology (direct) but may also include how climate impacts shift vegetation in the boreal biome and then affect bird occurrence (indirect).

From the point of view of coniferous-associated species, refugia will likely be determined by the presence of spruce trees, which are limited by climate, particularly CMI, over the long term. In the short term, spruce forests may persist despite unsuitable climate conditions and continue to provide habitat for many species. As white spruce is highly significant species for coniferous-associated species, it represents major a mediator of climate effects (at both large and small scales) on birds. With increasing warming temperatures and northward shifts of parkland-like forests (i.e., higher abundance of deciduous trees, interspersed with grasslands; Price et al., 2013; Schneider, 2013), our results suggest that coniferous-associated birds are more likely than other groups to decrease in occurrence as white spruce forests are lost. Given the strong direct effects of climate that we found, cooler and wetter climates (i.e., higher CMI) may also benefit coniferous-associated species directly, either through physiological mechanisms or via other unmeasured variables such as prey availability. These results suggests that the persistence of spruce trees may not be sufficient for many bird species, once climate conditions become unsuitable.

The implications of our findings for wetland-associated species may be like those for conifer-associated species, as the directionality of the results was similar. For this group, refugia will clearly depend on the persistence of wetlands and associated trees, particularly black spruce, which was an important variable and most influenced by climate (strong mediation effect) amongst the tree species investigated. Because climate change is predicted to lead to extended drought in the western boreal, black spruce may eventually be replaced by drought-tolerant species such as pine (Burton and Cumming, 1995, Baltzer et al. 2022), therefore leading to negative effects on wetland-associated birds. Peatlands, a major component of wetlands in the boreal plains, may be buffered from climate change by eco-hydrological processes, such that black spruce loss from lowland areas may be delayed (Stralberg et al. 2020). However, the large direct influence of climate in our models suggests that peatland persistence may be insufficient to prevent the decline of wetland-associated bird species.

For deciduous-associated bird species, vegetation characteristics were found to be more limiting than climate, which suggests that this group could benefit from the expansion of hemi-boreal climates (Price *et al.*, 2013). Even though we found more support for the resource hypothesis for this group, the fact that climate had similar direct and indirect for some variables (e.g., CMI) suggests that other unmeasured factors may be important limiting factors for deciduous-associated species, partially suggesting support for the physiology hypothesis as well, and indicate that this group is susceptible to climate impacts via effects on the vegetation they occupy. Deciduous trees generally grow and respond to climate faster than evergreens (Drobyshev *et al.*, 2013), but they are also sensitive to drought (Hogg et al., 2002), which is expected to be pervasive problem in the boreal plains by the end of the century (Price et al., 2013). This fast response to climate means that even though deciduous-associated species may benefit from warming, they may still be affected by climate change, depending on the fate of deciduous tree species such as aspen, and the extent to which they will be water-limited in the future.

It is important to note that we only adjusted T_{min} and CMI to incorporate topographic and forest cover impacts on climate at the local scale, which may have implications for the results relative to previous work (e.g., Stralberg *et al.*, 2018). To some degree, our results for conifer-associated species supports the notion that local available moisture is a major limiting factor for some species (Stralberg *et al.*, 2018). Whether the strength of influence would change if we had used non-adjusted climate variables (i.e., macroclimate), remains unclear. Another limitation of our approach may involve the way SEMs estimate mediation effects, which can have implications on how effect sizes are presented (Shipley, 2009). Estimates for a given mediator represent the sum of all indirect paths that involves it. Mediator impacts could be evaluated by looking at individual predictor variables and how their impact is partitioned among the different mediators (e.g., CMI → trees → bird occurrence). This methodology means that the mediation role of each vegetation variable varies by climate variable of interest. We opted to provide a fulsome picture of mediators and indirect effects, which even though it may hide the strength of individual indirect effects, still provides an overall picture of the importance of each mediator. Finally, other unmeasured habitat features may also be affected by climate, such that other aspects of forest composition and structure, as well as factors like prey availability and other species interactions, could also mediate the impacts of climate (Khaliq *et al.*, 2017). Therefore, could mean that climate variables could be affecting songbirds more indirectly than indicated by our models, with implications for the rate of climate-driven changes in bird communities.

Conclusion

Our results suggest the potential for rapid change in boreal songbird communities, given the stronger direct effects of climate relative to the indirect effects. The stronger impact of vegetation on coniferous- and deciduous-associated species also suggests that climate change impacts on habitat will have strong impacts on occurrence of these species, irrespective of impacts on their physiology. Coniferous -associated species may be more threatened by climate change because of their association with cold-adapted forests (e.g., white spruce dominated forests). Mature forests could then play a significant role in reducing that threat as that is associated with climate buffering, irrespective of nesting habitat preferences (De Frenne *et al.*, 2019; De Lombaerde *et al.*, 2022). Importantly, deciduous-associated species may be able to shift distributions more rapidly than species associated with mature and coniferous forests given the expected transition from coniferous to early-seral and aspen dominated landscapes in the boreal plains (Price *et al.*, 2013; Stralberg *et al.*, 2015). This faster transition to deciduous-dominated landscapes would put coniferous-associated species at higher risk to climate change. With delays in vegetation transitions, transient bird communities may emerge. Wetland-associated birds may also be more vulnerable to climate directly, but they might be buffered from climate change through processes that characterise peatland ecosystems, so it is pivotal to understand feedbacks of wetlands on climate so we can better understand how vulnerable this group is.

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Chapter 5 – General Discussion

Climate change refugia has been the common theme weaving the different chapters of this thesis together. Here I showed the connection between processes that affect climate conditions at the local scale and how these can translate to impact bird distribution and refugia potential in the context of a changing boreal ecosystem. I draw from different ecological theories to make these connections, but particularly from biogeography, physical and atmospheric sciences, and niche theory.

The importance and relevance of local climates is increasingly recognized in ecology (Hannah *et al.*, 2014; Suggitt *et al.*, 2018). Both biotic and abiotic properties can influence atmospheric conditions at a small scale, including vegetation and canopy cover (Chen, Franklin and Spies, 1993; Geiger, Aron and Todhunter, 1995; Bailey, 2009), and topography (e.g., aspect and landform; Thornthwaite, 1953; Barry and Blanken, 2016). Through a series of processes, conditions at local scales can deviate from conditions at larger scales. Dobrowski (2010) speaks about processes that can lead the boundary layer (the layer of air near the earth's surface) to be uncorrelated with the free atmosphere, including aspect, relief (roughness), elevation and drainage. The premise is that some of these features can lead the climate at the local scale to be resilient from changes that happen at larger scales, therefore yielding refugia (Dobrowski, 2011; Ashcroft *et al.*, 2012).

Despite the minimal relief that gives name to the boreal plains of western Canada, local climate conditions in hills and valley systems promote thermal heterogeneity to some extent. In Chapter 2, I investigated potential drivers of climate variability along the boreal–grassland transition zone in western Canada and found that local topography and vegetation had significant buffering effects on local climates. For example, topographically shaded sites were between 0.7 – 2.9 ˚C cooler than flat, exposed sites. These effects were smaller than what has been found in mountain systems (Geiger, Aron and Todhunter, 1995; Gruber, Hoelzle and Haeberli, 2004; Huang *et al.*, 2008; Suggitt *et al.*, 2011), both in steep terrain (e.g., 6 ˚C in the Swiss Alps, Gruber, Hoelzle and Haeberli, 2004) and smaller mountains of approximately ~300 m in elevation (7 ˚C in Wales and England, Suggitt *et al.*, 2011). I attributed these differences to a few factors, such as slope angle, or even instrumentation (Geiger, Aron and Todhunter, 1995, Maclean *et al.*, 2021), but highlight that the differences observed here were substantial. Sites with more surrounding forest cover were almost 1 ˚C cooler on average in summer and 2 ˚C warmer in winter than non-forested sites, consistent with other studies from boreal forests (De

Frenne *et al.*, 2021). This impact varied by different types of canopy cover and deciduous-dominated areas showed to be warmer in some cases, which I attributed to the different moisture-limited conditions that characterize the boreal-parkland-grassland transition zone (e.g., Koster *et al.*, 2004; Seneviratne *et al.*, 2010). For example, coniferous forest canopies have higher aerodynamic roughness relative to deciduous dominated forests, which could lead to a decrease in air temperature locally (McCaughey *et al.*, 1997; Blanken *et al.*, 2001). In general, levels of surrounding coniferous and mixedwood forest had a negative effect on mean summer temperature. Areas with greater terrain roughness experienced maximum temperatures that were up to 1.62 ˚C cooler, which demonstrates both that the vertical and horizontal mixing of air in slopes at the local level can reduce temperature extremes near the surface (Gloyne, 1967). By extension, I demonstrated that local topographic effects on temperature, captured by my dataloggers, were not fully captured in commonly used downscaled gridded climate data products. Interestingly, I found that elevation had mostly no noticeable influence on the difference, which suggested to me that models captured the effects of that variable very well, but the magnitude of the difference between the two estimates was greatest in areas where my models predicted warmer temperatures (e.g., exposed and/or non-forested slopes). This difference highlighted that local ecosystem functioning and landscape properties that modify the climate at larger scales (mesoclimate; Geiger, Aron and Todhunter, 1995; Chen *et al.*, 1999; Bailey, 2009), were not captured in gridded climate products.

Overall, results from Chapter 2 suggest that the combination of forest cover and topographic setting has the potential to buffer the effects of near-term climate change, although the level of future persistence is uncertain (Lembrechts and Nijs, 2020; Zellweger *et al.*, 2020; De Frenne *et al.*, 2021; De Lombaerde *et al.*, 2022). My results provide empirical support for the notion that topographically- and vegetation-mediated temperature variation may result in microrefugia within the southern boreal zone (Stralberg *et al*., 2020). How these local processes would unfold to influence the distribution of species in the boreal plains remains uncertain. I know that niche defines species ranges by a suite of macroclimate factors that constrain species' physiology, while at finer scales, local factors become increasingly more important to determine species occurrence (Guisan and Thuiller, 2005). Climate is one of the main factors defining species' niche, and by extent their range and distribution (Guisan and Thuiller, 2005; Thuiller *et al*., 2008). In a changing climate, where the boreal forest may see unprecedented change in forest composition and conditions (Price *et al*., 2013), understanding if local climate conditions will lead to more (or less) refugia becomes an increasingly important question. However, the mechanism by which climate can influence the distribution, occurrence and richness of species can be hypothesized to be physiological (direct) or related to impacts on resource use and availability (indirect) (Ferger *et al.*, 2014). Directly, climate can limit species because of energy availability, which is used to maintain their body within their thermoneutral zone (Currie *et al.*, 2004; Buckley, Hurlbert and Jetz, 2012). In extreme circumstances, such as extreme weather events, climate can also directly affect recruitment and fecundity of birds (Fisher *et al.*, 2015; Dunn and Møller, 2019). Indirectly, the effects of climate may occur via its effects on vegetation, which in turn cascade to influence birds (Ferger *et al.*, 2014).

In Chapter 3, I investigated the impact of local climates on the predicted distribution and refugia potential for multiple songbird groups (coniferous-, deciduous- and wetland-associated species). By using the results from Chapter 2 to build climate offsets and therefore adjust gridded products to local processes, I found that the importance of climate variables, model explanatory power, and overall area of predicted refugia changed depending on whether adjusted or non-adjusted climate variables were used. Although the changes varied by songbird group, this suggested that topography does influence local climates in a way that can be detected for some bird species. This is quite remarkable, considering that topography and terrain roughness are quite limited in the boreal plains, but still led to detectable outcomes. My results suggest that the predicted total refugia potential area for most groups changed substantially after adjusting climate variables across groups or between model types (climate-only vs full). These findings partially supported my expectation that models with adjusted climate would identify more refugia. Part of that expectation comes from previous literature on microclimates, which indicated that microclimate may pick up more of the variation in factors influencing species distribution than macroclimate alone and improve model performance (Storlie *et al.*, 2013; Slavich *et al.*, 2014). My results suggested that some bird groups may be more or less sensible to these local processes. I conclude that different groups of species, and their intrinsic relationship with their habitat, plays an important role into how they are affected by local climate, and therefore, how much refugia is available to them. I think that there seems to be an interesting interface between habitat, local climate, and macroclimate to drive the amount of refugia predicted for coniferous- and deciduous-associated species. For coniferous-associated species, local climate plays a bigger role without considering habitat. Local climate conditions may be particularly influential for conifer-associated species because some climate variables became more important when I adjusted climate to the local scale. Meanwhile, vegetation, habitat, and macroclimate are more important drivers of refugia for deciduous-associated species. Finally, wetland-associated species seem to be more influenced by macroclimate, regardless of habitat effects.

In Chapter 4, I partially disentangled the mechanism by which climate can define habitat for boreal trees and, by extension, boreal songbird species. More specifically, my objective was to understand the direct and indirect limiting factors for songbird occurrence in at the southern margins of the western boreal region, which may inform our understanding of bird responses to climate change, including refugia. To do this, I used structural equation models to simultaneously model the occurrence of songbirds and biomass of trees as a function of climate and forest structure. This procedure allowed me to estimate direct and indirect effects of climate, as well as understand the role that trees play in mediating those indirect effects, as of plant attributes respond directly to climate, then affecting different aspects wildlife. Overall, my results indicate that the direct effects of climate were substantially stronger than the indirect effects for coniferous- and wetland-associated species, but for deciduous-associated birds the indirect impacts were sometimes comparable in strength with other direct climate factors. Concluding that these direct impacts are the result of a physiological response by birds may still require further research though. As I indicated earlier, climate may impact birds physiologically in extreme climate circumstances, but not so much otherwise (Hawkins et al., 2003; McCain, 2007, 2009; McKechnie & Wolf, 2010; Buckley et al., 2012), which could suggest that such strong direct effects of climate could in fact be unmeasured or unaccounted effects of vegetation structure.

I see some congruence between the results from Chapter 3 and 4. Although I did not explore the impacts of local climates specifically via the structural equation models, I can see that climate is a very important aspect of refugia potential for conifer-associated bird species at the local scale (Chapter 3), and probability of occurrence more broadly (Chapter 4). Wetland-associated species refugia potential seems to be heavily driven by macroclimate, which was also confirmed by my structural equation models. My species distribution models (Chapter 3) suggested that vegetation, habitat, and macroclimate drive deciduous-associated species. For example, the relative influence of climate variables dropped substantially after adjusting for local topographic and tree cover effects for deciduous. Moreover, I found that some of the climate effects on this group seem to be indirect via vegetation, in comparable size to the direct effects of climate, such as CMI (Chapter 4). This still can be a product of unmeasured factors but may hint at which bird groups may be more exposed to the detrimental effects of climate change and which ones might be more sensitive to it. For example, phenological sensitivity to climate change, the capacity for species to change in their seasonal timing (Thackeray *et al.*, 2016), is strongly associated with nesting habitat for bird populations (Bailey *et al.*, 2022). Populations associated with deciduous forests can have higher phenological sensitivity than populations occupying coniferous-dominated forests (Bailey *et al.*, 2022). One of the reasons might be that coniferous forests have a wider period of peak food abundance and generally lower food abundance than deciduous-dominated forest (Blondel *et al.*, 1993). A narrower phenological window may create selective pressure on birds to synchronize breeding with temperature cues, making them more sensitive to climate (Visser and Gienapp, 2019). The level of climate change exposure may also impact their level of phenological sensitivity, where bird populations most exposed to climate change over the last few decades seem to be less sensitive to climatic variation (Bailey *et al.*, 2022). Since exposure to climate change increases with latitude, northerly populations of birds, such as the ones in the boreal plains, may have generally low capacity to avoid the negative impacts of climate change, and may be declining more rapidly (Jiguet *et al.*, 2007; Serreze and Barry, 2011; Foden *et al.*, 2013; Bailey *et al.*, 2022).

Conservation implications

Species most vulnerable to climate change may require direct intervention including conservation measures (Foden *et al.*, 2013). Based on my results from Chapter 3 and 4, I believe that coniferous- and wetland-associated species may be particularly at risk because they may lack the ability to adapt to climate change and be more impacted by climate directly, especially because key tree species, such as spruce, may be replaced by fast-growing deciduous trees in the future. The vulnerability of coniferous-associated species to climate change has been reported by other studies in the boreal biome that projected severe declines in abundance by the end of the century (Cadieux *et al.*, 2020), which support my observations in both chapters. I think that refugia potential identification at smaller scales may be crucial for this group and may indicate that areas with highest refugia potential could be prioritized for conservation, such as the creation of protected areas as suggested by Stralberg *et al.* (2019).

Wetland-associated species have seen overall declines in population growth in other boreal forests (Laaksonen and Lehikoinen, 2013) and may be facing a similar fate in boreal North America. Wetlands may persist in northern latitudes because moisture may persist for longer in cold temperatures, but they will succumb to drying, and so will birds. The distribution of wetlands plays a major role for boreal birds, particularly because of heterogeneity at the local level (Calmé and Desrochers, 2000). I then think that the conservation of wetland-associated species may be better captured by examining refugia potential at macro scales (i.e., macrorefugia), while considering differences in habitat at the local level (Stralberg *et al.*, 2019).

Deciduous-associated species may be able to track some of the phenology and changes in environment that will follow with climate change (Bailey *et al.*, 2022). Meanwhile, the expected changes in southern margin of the boreal, especially the northerly expansion of the hemi-boreal and parkland biomes (Price *et al.*, 2013) may in fact benefit them. Nonetheless, the boreal biome is at higher risk due to exposure to climate change, low capacity for adaptation, and rapid climate velocity (Foden *et al.*, 2013; Hamann *et al.*, 2015), so deciduous-associated species are still vulnerable to climate impacts. Delineating refugia potential areas for this group might be slightly more difficult compared to the other ones, but may nonetheless require conservation of high potential areas defined by habitat and tree composition.

The effectiveness of conservation measures also depends on the vulnerability and sensitivity to climate change at the species level (Stralberg *et al.*, 2019). In retrospect, when I discussed the conservation of species groups instead of individual species may leave out important aspects of species life-history traits that play a role in their level of vulnerability to climate change. For example, the level of microhabitat specialization may heighten the vulnerability of a species (Foden *et al.*, 2013), which has been seen in some boreal-forest specialists (Ralston and Kirchman, 2013). Still, I believe that my approach captured important aspects of species life-history, which was confirmed by the directionality of tree effects on a given group.

Further research is needed to understand the impacts that changes in tree species composition due to climate warming might have on the distribution and identification of refugia potential for songbirds. More importantly, it is urgent that I understand how forests will change and how quickly. The strength of ecological inertia to maintain forests longer than climate models predict is still unknown. Research indicates that the amount of habitat that a species can reach could be mostly driven by changes in tree species composition (Lalechère and Bergès, 2022), which reinforces the premise that refugia potential for forest birds is intrinsically related to where forests will be (Stralberg *et al.*, 2018). Therefore, simultaneously modelling the impacts of climate change on species distribution and on their habitat may provide further clues to optimize conservation measures. Forest dynamics models can help get at this, but they have certain limitations, including parameterization and uncertainties in the modelling approach.

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Appendix

Appendix S1

Table S1.1: Model ranking and standardized coefficients for all temperature metrics for the summer and winter months between 2014 and 2020 in river valley and hill systems in Alberta, Canada. Only the top three models are presented. Please refer to Table 1.2 for variables in each model. K - number of parameters, ω - weighted AICc of the model, LL - negative log-likelihood. * denotes significant coefficients at α=0.05.

									Standardized β Coefficient										
Season	**Metric**	**Model Name**	**K**	**ΔAICc**	**ω**	**LL**	**R2m**	**R2c**	**Intercept**	**Elevation**	**Lat**	**Solar Radiation**	**Incised Valleys**	**Ridge Top**	**Ter. Roughness Index**	**Comp. Topo. Index**	**Broadleaf**	**Conifer**	**Mixedwood**
Summer	T_{max}	Topodiversity and Vegetation	17	0.00	0.55	-2451.64	0.39	0.84	22.68 *	-1.41 *	-3.38 *	0.53 *	-0.3 *	-0.28 *	-0.22 *	-	0.24 *	0.15	0.02
		Full	18	1.42	0.27	-2451.32	0.39	0.84	22.67 *	-1.42 *	-3.37 *	0.53 *	-0.26 *	-0.29 *	-0.24 *	-0.04	0.24 *	0.15	0.01
		Topodiversity	14	2.28	0.18	-2455.86	0.39	0.84	22.6 *	-1.48 *	-3.22 *	0.52 *	-0.34 *	-0.25 *	-0.21 *	-	-	-	-
		Aspect	11	20.94	0.00	-2468.25	0.40	0.83	22.38 *	-1.47 *	-3.21 *	0.5 *	-	-	-	-	-	-	-
		Elevation	10	123.32	0.00	-2520.46	0.42	0.82	22.35 *	-1.53 *	-3.41 *	-	-	-	-	-	-	-	-
		Moisture and Landform	13	123.58	0.00	-2517.53	0.42	0.83	22.51 *	-1.48 *	-3.4 *	-	-0.23	-0.24 *	-	0.02	-	-	-

Season	Metric	Model Name	K	ΔAICc	ω	LL	R2m	R2c	Standardized β Coefficient										
									Intercept	Elevation	Lat	Solar Radiation	Incised Valleys	Ridge Top	Ter. Roughness Index	Comp. Topo. Index	Broadleaf	Conifer	Mixedwood
		Null	9	172.42	0.00	-2546.03	0.37	0.83	22.99 *	-	-2.77 *	-	-	-	-	-	-	-	-
	T_{99}	Topodiversity	14	0.00	0.54	-3189.71	0.33	0.74	31.2 *	-1.49 *	-3.95 *	0.66 *	-0.5 *	-0.54 *	-0.28 *	-	-	-	-
		Topodiversity and Vegetation	17	1.73	0.23	-3187.50	0.33	0.75	31.26 *	-1.64 *	-4.21 *	0.7 *	-0.48 *	-0.54 *	-0.3 *	-	0.23	0.33	0.03
		Full	18	1.77	0.22	-3186.49	0.33	0.74	31.23 *	-1.66 *	-4.19 *	0.7 *	-0.34	-0.55 *	-0.33 *	-0.14	0.22	0.33	0.02
		Aspect	11	11.05	0.00	-3198.30	0.34	0.73	30.77 *	-1.65 *	-4.02 *	0.64 *	-	-	-	-	-	-	-
		Moisture and Landform	13	59.47	0.00	-3220.47	0.36	0.73	31.07 *	-1.49 *	-4.16 *	-	-0.26	-0.54 *	-	-0.05	-	-	-
		Elevation	10	60.57	0.00	-3224.08	0.36	0.73	30.74 *	-1.71 *	-4.27 *	-	-	-	-	-	-	-	-
		Null	9	80.82	0.00	-3235.22	0.32	0.74	31.44 *	-	-3.48 *	-	-	-	-	-	-	-	-
	T_{min}	Topodiversity and Vegetation	17	0.00	0.63	-1784.97	0.09	0.84	10.04 *	-0.49 *	-0.11	-0.04	-0.27 *	0.41 *	0.13 *	-	-0.18 *	-0.23 *	-0.19 *
		Full	18	1.03	0.37	-1784.45	0.09	0.84	10.03 *	-0.5 *	-0.11	-0.04	-0.24 *	0.41 *	0.12 *	-0.03	-0.18 *	-0.23 *	-0.19 *
		Topodiversity	14	27.93	0.00	-1802.01	0.04	0.82	10.15 *	-0.38 *	-0.2	-0.01	-0.2 *	0.4 *	0.11 *	-	-	-	-
		Moisture and Landform	13	38.00	0.00	-1808.07	0.04	0.81	10.17 *	-0.41 *	-0.2	-	-0.2 *	0.4 *	-	-0.05	-	-	-

									Standardized β Coefficient										
Season	Metric	Model Name	K	ΔAICc	ω	LL	R2m	R2c	Intercept	Elevation	Lat	Solar Radiation	Incised Valleys	Ridge Top	Ter. Roughness Index	Comp. Topo. Index	Broadleaf	Conifer	Mixedwood
		Elevation	10	100.92	0.00	-1842.58	0.01	0.78	10.45 *	0.19	0.11	-	-	-	-	-	-	-	-
		Null	9	101.49	0.00	-1843.89	0.00	0.78	10.38 *	-	0.01	-	-	-	-	-	-	-	-
		Aspect	11	102.95	0.00	-1842.58	0.01	0.78	10.45 *	0.19	0.11	0	-	-	-	-	-	-	-
Summer	T_{mean}	Topodiversity and Vegetation	17	0.00	0.73	-1469.74	0.37	0.95	15.9 *	-1.13 *	-1.79 *	0.12 *	-0.27 *	0.11 *	-0.05 *	-	-0.1 *	-0.16 *	-0.13 *
		Full	18	1.99	0.27	-1469.71	0.37	0.95	15.9 *	-1.13 *	-1.79 *	0.12 *	-0.28 *	0.11 *	-0.05 *	0.01	-0.1 *	-0.16 *	-0.13 *
		Topodiversity	14	24.29	0.00	-1484.96	0.34	0.95	15.97 *	-1.08 *	-1.85 *	0.14 *	-0.23 *	0.11 *	-0.06 *	-	-	-	-
		Aspect	11	51.05	0.00	-1501.41	0.32	0.94	16.04 *	-0.78 *	-1.73 *	0.14 *	-	-	-	-	-	-	-
		Moisture and Landform	13	74.32	0.00	-1511.00	0.36	0.95	15.96 *	-1.08 *	-1.95 *	-	-0.22 *	0.11 *	-	0.03	-	-	-
		Elevation	10	92.73	0.00	-1523.27	0.33	0.94	16.04 *	-0.79 *	-1.81 *	-	-	-	-	-	-	-	-
		Null	9	162.77	0.00	-1559.30	0.30	0.93	16.37 *	-	-1.44 *	-	-	-	-	-	-	-	-
	GDD_5	Topodiversity and Vegetation	17	0.00	0.62	-7406.31	0.29	0.84	422.66 *	-56.84 *	-134.06 *	-2.4	-3.72	2.26	-6.62 *	-	-10.42 *	-9.87 *	-9.91 *
		Full	18	1.39	0.31	-7405.97	0.29	0.84	423.22 *	-56.45 *	-134.21 *	-2.44	-5.85	2.41	-6.01 *	2.23	-10.18 *	-9.79 *	-9.79 *

									Standardized β Coefficient										
Season	**Metric**	**Model Name**	**K**	**ΔAICc**	**ω**	**LL**	**R2m**	**R2c**	**Intercept**	**Elevation**	**Lat**	**Solar Radiation**	**Incised Valleys**	**Ridge Top**	**Ter. Roughness Index**	**Comp. Topo. Index**	**Broadleaf**	**Conifer**	**Mixedwood**
		Topodiversity	14	5.26	0.04	-7412.02	0.27	0.84	429.25 *	-47.18 *	-136.59 *	-1.17	0.17	0.79	-7.82 *	-	-	-	-
		Elevation	10	8.23	0.01	-7417.58	0.27	0.84	427.45 *	-48.86 *	-138.43 *	-	-	-	-	-	-	-	-
		Aspect	11	9.66	0.00	-7417.28	0.28	0.84	427.43 *	-49.04 *	-139.63 *	-1.84	-	-	-	-	-	-	-
		Moisture and Landform	13	10.27	0.00	-7415.54	0.27	0.84	429.27 *	-44.66 *	-136.45 *	-	-1.62	0.31	-	4.93	-	-	-
		Null	9	25.87	0.00	-7427.42	0.25	0.85	447.22 *	-	-114.49 *	-	-	-	-	-	-	-	-
	T_{range}	Topodiversity and Vegetation	17	0.00	0.71	-2668.83	0.36	0.73	12.56 *	-1.02 *	-3.02 *	0.56 *	-0.13	-0.68 *	-0.35 *	-	0.34 *	0.34 *	0.19 *
		Full	18	2.06	0.25	-2668.83	0.36	0.73	12.56 *	-1.02 *	-3.02 *	0.56 *	-0.13	-0.68 *	-0.35 *	0	0.34 *	0.34 *	0.19 *
		Topodiversity	14	5.64	0.04	-2674.72	0.38	0.70	12.38 *	-1.17 *	-2.79 *	0.52 *	-0.22	-0.64 *	-0.31 *	-	-	-	-
		Aspect	11	49.24	0.00	-2699.59	0.42	0.68	11.85 *	-1.67 *	-3.02 *	0.49 *	-	-	-	-	-	-	-
		Moisture and Landform	13	98.50	0.00	-2722.18	0.40	0.68	12.27 *	-1.16 *	-2.94 *	-	-0.13	-0.64 *	-	0.08	-	-	-
		Elevation	10	114.17	0.00	-2733.07	0.43	0.67	11.82 *	-1.73 *	-3.2 *	-	-	-	-	-	-	-	-
		Null	9	157.92	0.00	-2755.96	0.34	0.69	12.54 *	-	-2.44 *	-	-	-	-	-	-	-	-

									Standardized β Coefficient										
Season	Metric	Model Name	K	ΔAICc	ω	LL	R2m	R2c	Intercept	Elevation	Lat	Solar Radiation	Incised Valleys	Ridge Top	Ter. Roughness Index	Comp. Topo. Index	Broadleaf	Conifer	Mixedwood
Winter	T_{max}	Topodiversity and Vegetation	17	0.00	0.40	-1839.46	0.33	0.93	-4.97 *	0.22	-2.87 *	0.34 *	-0.28 *	0.01	0.06	-	0.04	-0.08	0.06
		Full	18	0.03	0.40	-1838.44	0.33	0.93	-4.98 *	0.22	-2.87 *	0.34 *	-0.23 *	0.01	0.05	-0.06	0.04	-0.07	0.06
		Topodiversity	14	1.37	0.20	-1843.24	0.32	0.93	-5.01 *	0.04	-2.95 *	0.35 *	-0.31 *	0.02	0.06	-	-	-	-
		Aspect	11	15.75	0.00	-1853.50	0.33	0.93	-4.96 *	0.35 *	-2.78 *	0.35 *	-	-	-	-	-	-	-
		Moisture and Landform	13	88.38	0.00	-1887.77	0.34	0.93	-4.99 *	0.05	-3.1 *	-	-0.26 *	0.02	-	-0.07	-	-	-
		Elevation	10	100.79	0.00	-1897.04	0.34	0.93	-4.93 *	0.36 *	-2.94 *	-	-	-	-	-	-	-	-
		Null	9	103.26	0.00	-1899.30	0.34	0.93	-5.09 *	-	-3.14 *	-	-	-	-	-	-	-	-
	T_{99}	Full	18	0.00	0.80	-2724.59	0.18	0.32	4.64 *	-0.06	-3.13 *	0.39 *	-0.64 *	-0.11	0.45 *	0.18 *	-0.62 *	-0.7 *	-0.49 *
		Topodiversity and Vegetation	17	2.83	0.20	-2727.04	0.18	0.32	4.62 *	-0.06	-3.1 *	0.39 *	-0.47 *	-0.13	0.4 *	-	-0.62 *	-0.7 *	-0.5 *
		Topodiversity	14	35.91	0.00	-2746.67	0.18	0.32	4.91 *	0.15	-3.44 *	0.49 *	-0.29	-0.15	0.32 *	-	-	-	-
		Aspect	11	51.87	0.00	-2757.73	0.18	0.31	4.89 *	0.26	-3.38 *	0.49 *	-	-	-	-	-	-	-
		Null	9	87.81	0.00	-2777.74	0.18	0.32	4.82 *	-	-3.67 *	-	-	-	-	-	-	-	-

									Standardized β Coefficient										
Season	**Metric**	**Model Name**	**K**	**ΔAICc**	**ω**	**LL**	**R2m**	**R2c**	**Intercept**	**Elevation**	**Lat**	**Solar Radiation**	**Incised Valleys**	**Ridge Top**	**Ter. Roughness Index**	**Comp. Topo. Index**	**Broadleaf**	**Conifer**	**Mixedwood**
		Moisture and Landform	13	88.94	0.00	-2774.22	0.18	0.33	5.01 *	-0.01	-3.69 *	-	-0.53 *	-0.09	-	0.09	-	-	-
		Elevation	10	89.22	0.00	-2777.42	0.19	0.32	4.93 *	0.27	-3.53 *	-	-	-	-	-	-	-	-
	T_{min}	Full	18	0.00	1.00	-2487.68	0.11	0.85	-12.51 *	1.46 *	-0.7	0.14	-0.25	0.17	-0.14	-0.28 *	0.5 *	0.3 *	0.37 *
		Topodiversity and Vegetation	17	12.03	0.00	-2494.73	0.11	0.85	-12.47 *	1.48 *	-0.75	0.15 *	-0.5 *	0.21	-0.05	-	0.51 *	0.3 *	0.38 *
		Moisture and Landform	13	19.26	0.00	-2502.46	0.09	0.84	-12.76 *	1.12 *	-0.61	-	-0.35	0.16	-	-0.27 *	-	-	-
		Topodiversity	14	33.28	0.00	-2508.44	0.08	0.84	-12.72 *	1.06 *	-0.66	0.09	-0.65 *	0.22	-0.02	-	-	-	-
		Elevation	10	46.37	0.00	-2519.08	0.11	0.84	-12.58 *	1.71 *	-0.32	-	-	-	-	-	-	-	-
		Aspect	11	47.15	0.00	-2518.45	0.11	0.84	-12.58 *	1.71 *	-0.29	0.08	-	-	-	-	-	-	-
		Null	9	84.14	0.00	-2538.99	0.05	0.83	-13.35 *	-	-1.28 *	-	-	-	-	-	-	-	-
Winter	T_{mean}	Full	18	0.00	0.99	-2095.69	0.18	0.91	-8.85 *	0.73 *	-1.79 *	0.18 *	-0.23	0.09	-0.11 *	-0.17 *	0.27 *	0.11	0.23 *
		Topodiversity and Vegetation	17	8.54	0.01	-2100.99	0.18	0.91	-8.83 *	0.73 *	-1.82 *	0.19 *	-0.38 *	0.11	-0.06	-	0.28 *	0.11	0.24 *
		Topodiversity	14	26.18	0.00	-2112.91	0.16	0.91	-8.99 *	0.39	-1.82 *	0.17 *	-0.48 *	0.12	-0.05	-	-	-	-

									Standardized β Coefficient										
Season	Metric	Model Name	K	ΔAICc	ω	LL	R2m	R2c	Intercept	Elevation	Lat	Solar Radiation	Incised Valleys	Ridge Top	Ter. Roughness Index	Comp. Topo. Index	Broadleaf	Conifer	Mixedwood
		Moisture and Landform	13	28.35	0.00	-2115.01	0.17	0.91	-9 *	0.47 *	-1.83 *	-	-0.28 *	0.09	-	-0.15 *	-	-	-
		Aspect	11	41.73	0.00	-2123.75	0.18	0.91	-8.91 *	0.86 *	-1.56 *	0.16 *	-	-	-	-	-	-	-
		Elevation	10	50.68	0.00	-2129.25	0.18	0.91	-8.89 *	0.87 *	-1.62 *	-	-	-	-	-	-	-	-
		Null	9	70.08	0.00	-2139.97	0.16	0.90	-9.29 *	-	-2.11 *	-	-	-	-	-	-	-	-
	GDD_5	Topodiversity	14	0.00	0.48	-2245.28	0.02	0.08	1.4 *	0.04	-1.36 *	0.19 *	-0.21 *	0.02	-0.03	-	-	-	-
		Topodiversity and Vegetation	17	1.56	0.22	-2242.97	0.02	0.08	1.36 *	0.04	-1.29 *	0.18 *	-0.25 *	0.02	-0.01	-	-0.11	-0.13 *	-0.04
		Aspect	11	1.75	0.20	-2249.23	0.02	0.08	1.44 *	0.29	-1.24 *	0.19 *	-	-	-	-	-	-	-
		Full	18	2.98	0.11	-2242.65	0.02	0.08	1.37 *	0.05	-1.29 *	0.18 *	-0.27 *	0.03	0	0.03	-0.11	-0.13 *	-0.04
		Moisture and Landform	13	31.16	0.00	-2261.89	0.02	0.08	1.42 *	0.05	-1.47 *	-	-0.25 *	0.03	-	0.04	-	-	-
		Elevation	10	33.45	0.00	-2266.11	0.02	0.08	1.45 *	0.29	-1.33 *	-	-	-	-	-	-	-	-
		Null	9	34.19	0.00	-2267.49	0.02	0.08	1.33 *	-	-1.49 *	-	-	-	-	-	-	-	-
	T_{range}	Full	18	0.00	1.00	-2193.60	0.39	0.64	7.61 *	-1.23 *	-2.05 *	0.19 *	-0.14	-0.22	0.19 *	0.27 *	-0.46 *	-0.4 *	-0.3 *

									Standardized β Coefficient										
Season	**Metric**	**Model Name**	**K**	**ΔAICc**	**ω**	**LL**	**R2m**	**R2c**	**Intercept**	**Elevation**	**Lat**	**Solar Radiation**	**Incised Valleys**	**Ridge Top**	**Ter. Roughness Index**	**Comp. Topo. Index**	**Broadleaf**	**Conifer**	**Mixedwood**
		Topodiversity and Vegetation	17	16.10	0.00	-2202.69	0.38	0.63	7.56 *	-1.26 *	-2.02 *	0.18 *	0.1	-0.26	0.11	-	-0.47 *	-0.4 *	-0.31 *
		Topodiversity	14	38.62	0.00	-2217.04	0.35	0.59	7.75 *	-1.09 *	-2.21 *	0.24 *	0.21	-0.27	0.06	-	-	-	-
		Moisture and Landform	13	39.42	0.00	-2218.47	0.36	0.61	7.84 *	-1.1 *	-2.34 *	-	-0.06	-0.23	-	0.24 *	-	-	-
		Aspect	11	40.90	0.00	-2221.25	0.36	0.60	7.61 *	-1.44 *	-2.4 *	0.25 *	-	-	-	-	-	-	-
		Elevation	10	56.06	0.00	-2229.85	0.37	0.61	7.63 *	-1.42 *	-2.49 *	-	-	-	-	-	-	-	-
		Null	9	92.39	0.00	-2249.04	0.31	0.60	8.23 *	-	-1.74 *	-	-	-	-	-	-	-	-

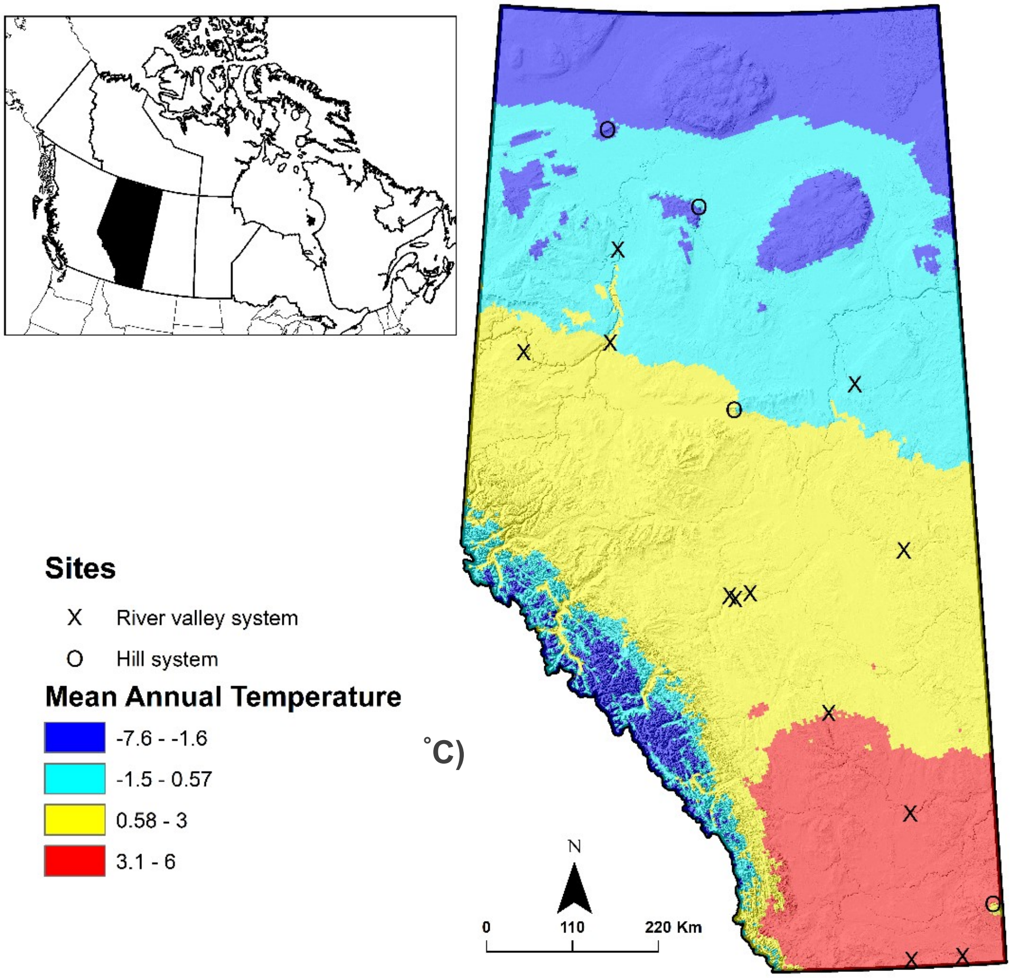


Figure S1.1: Mean annual temperature gradient and location of sampling sites in river and hill systems in Alberta, Canada.

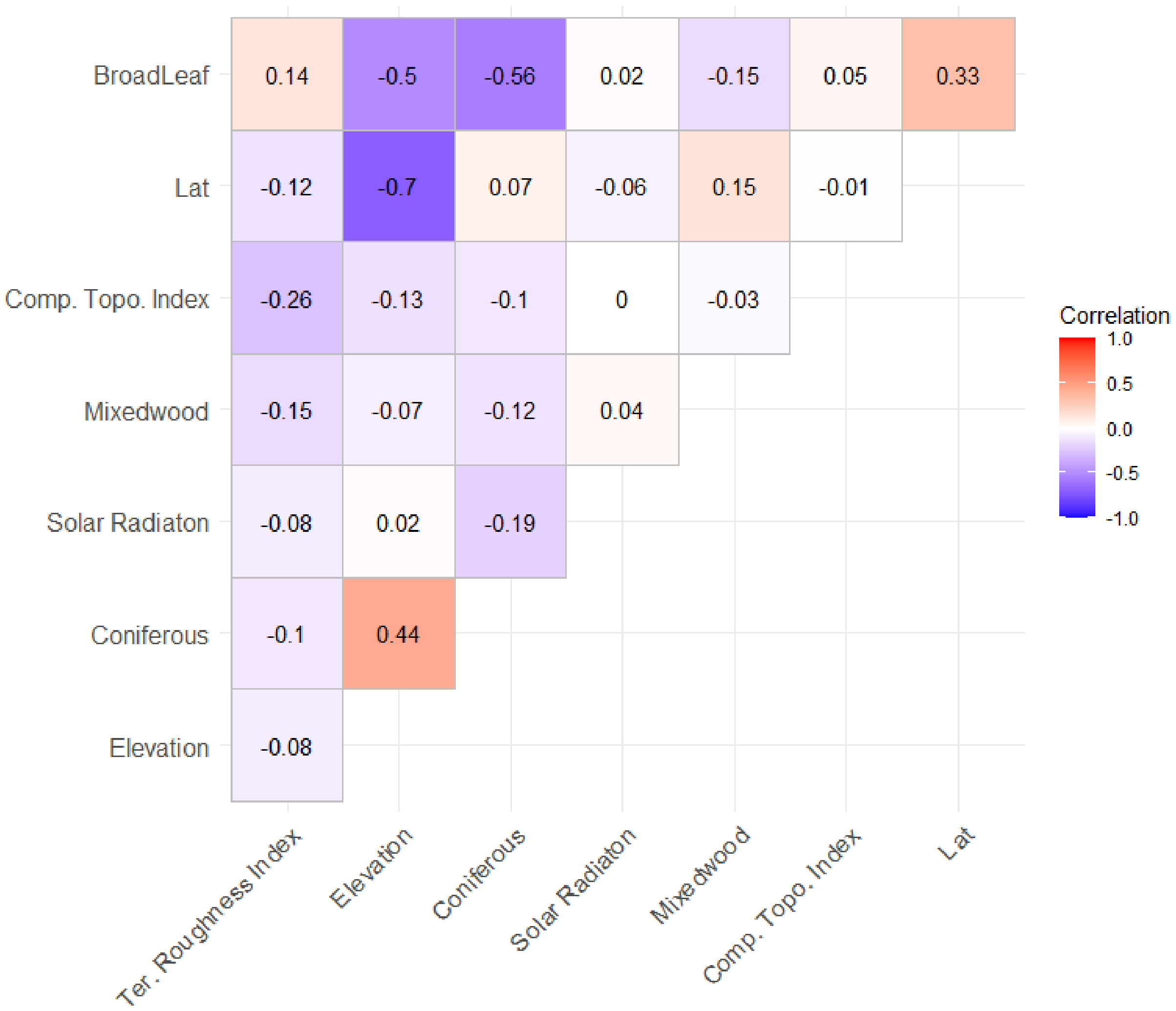
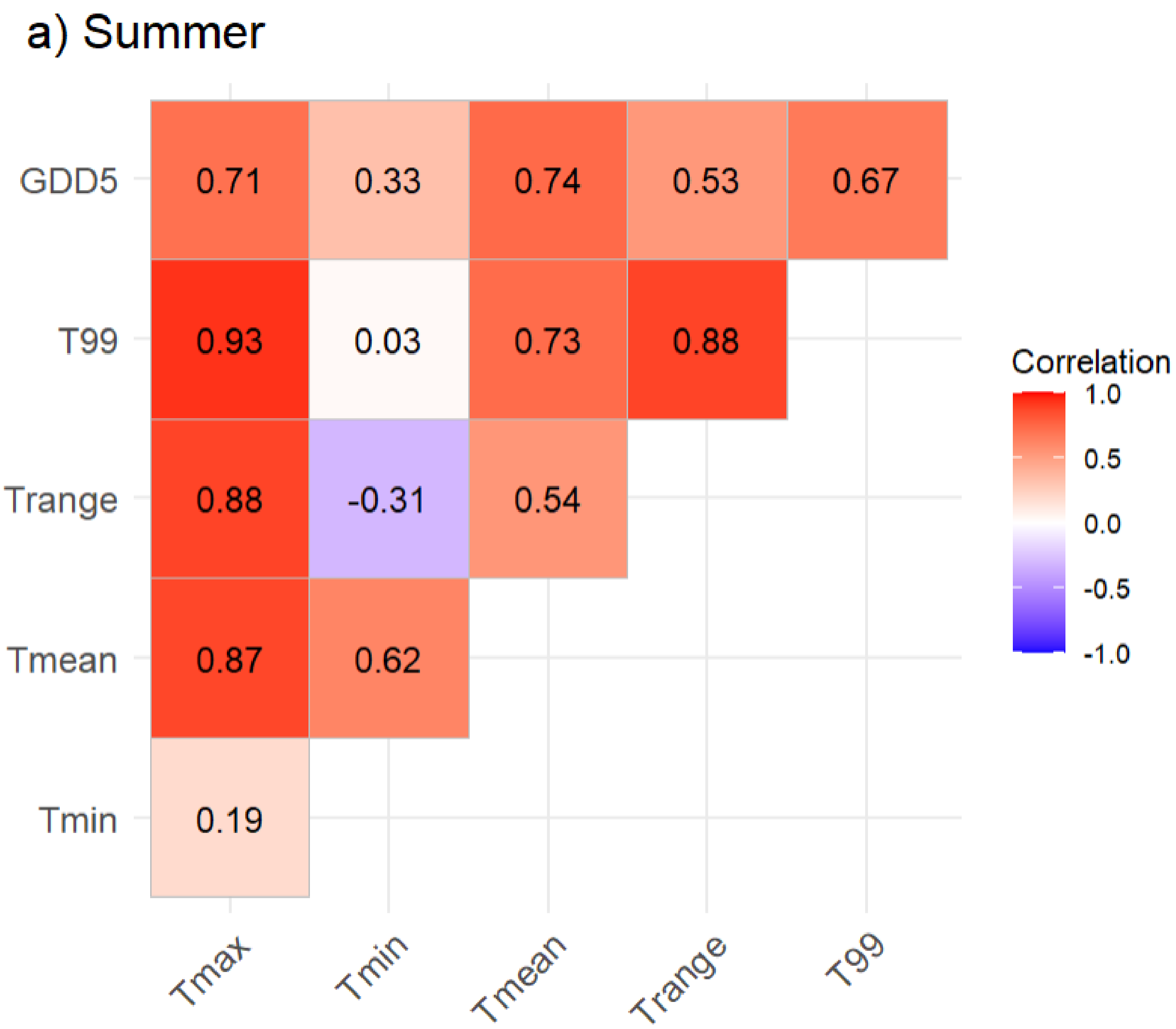


Figure S1.2: Correlation between continuous explanatory variables used in the linear mixed models. Comp. Topo. Index = Compound Topographic Index, Ter.

Roughness Index = Terrain Roughness Index, Lat = Latitude. Please refer to the main text for details about each variable.



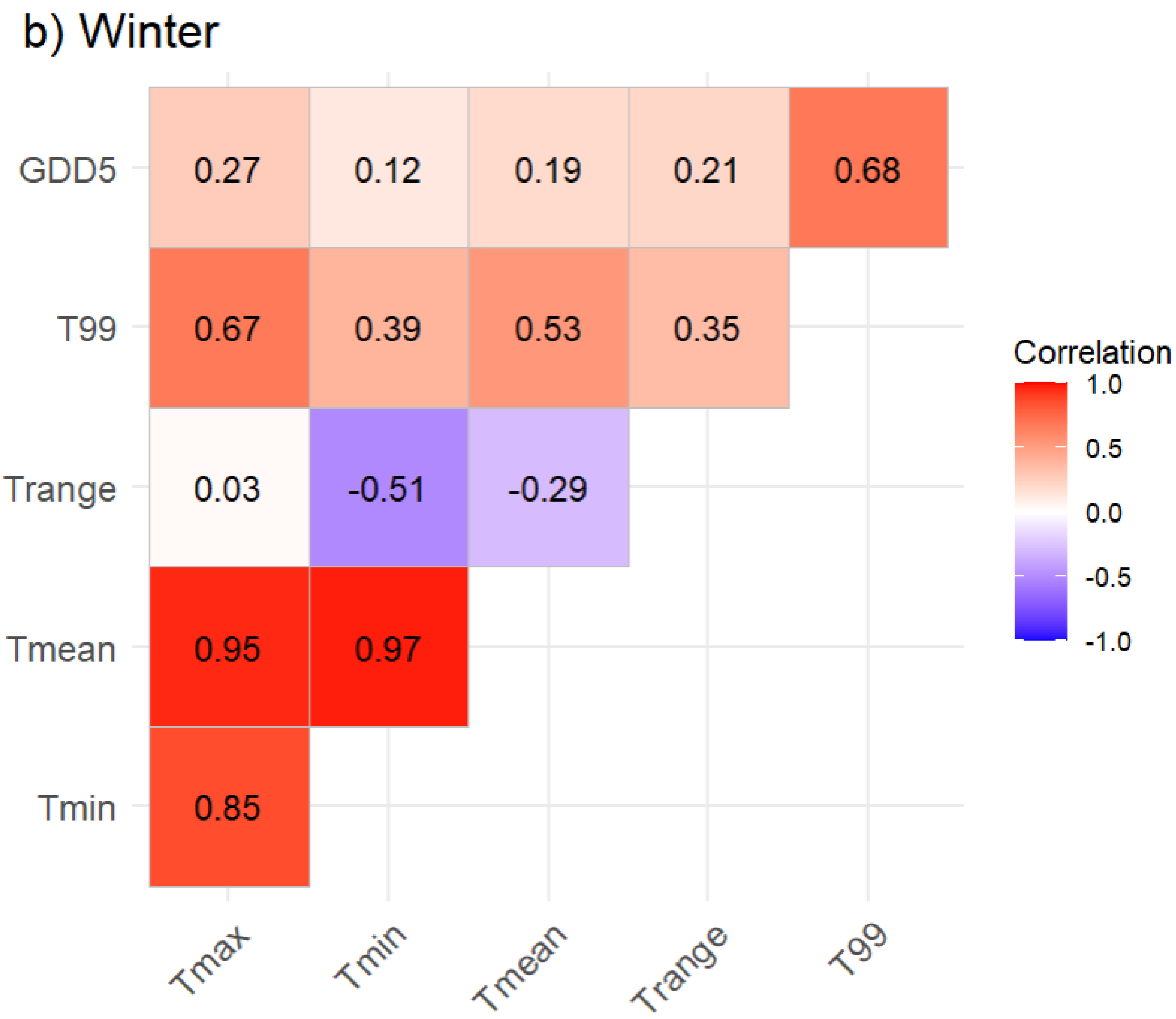


Figure S1.3: Correlation between continuous response variables used in the linear mixed models for the summer (a) and winter (b). Metrics represent monthly averages of daily maxima (T_{max}), minima (T_{min}), mean (T_{mean}), the 99th percentile of daily T_{max}, and

growing degree days above 5 ˚C (GDD5). Please refer to the main text for details about each metric.

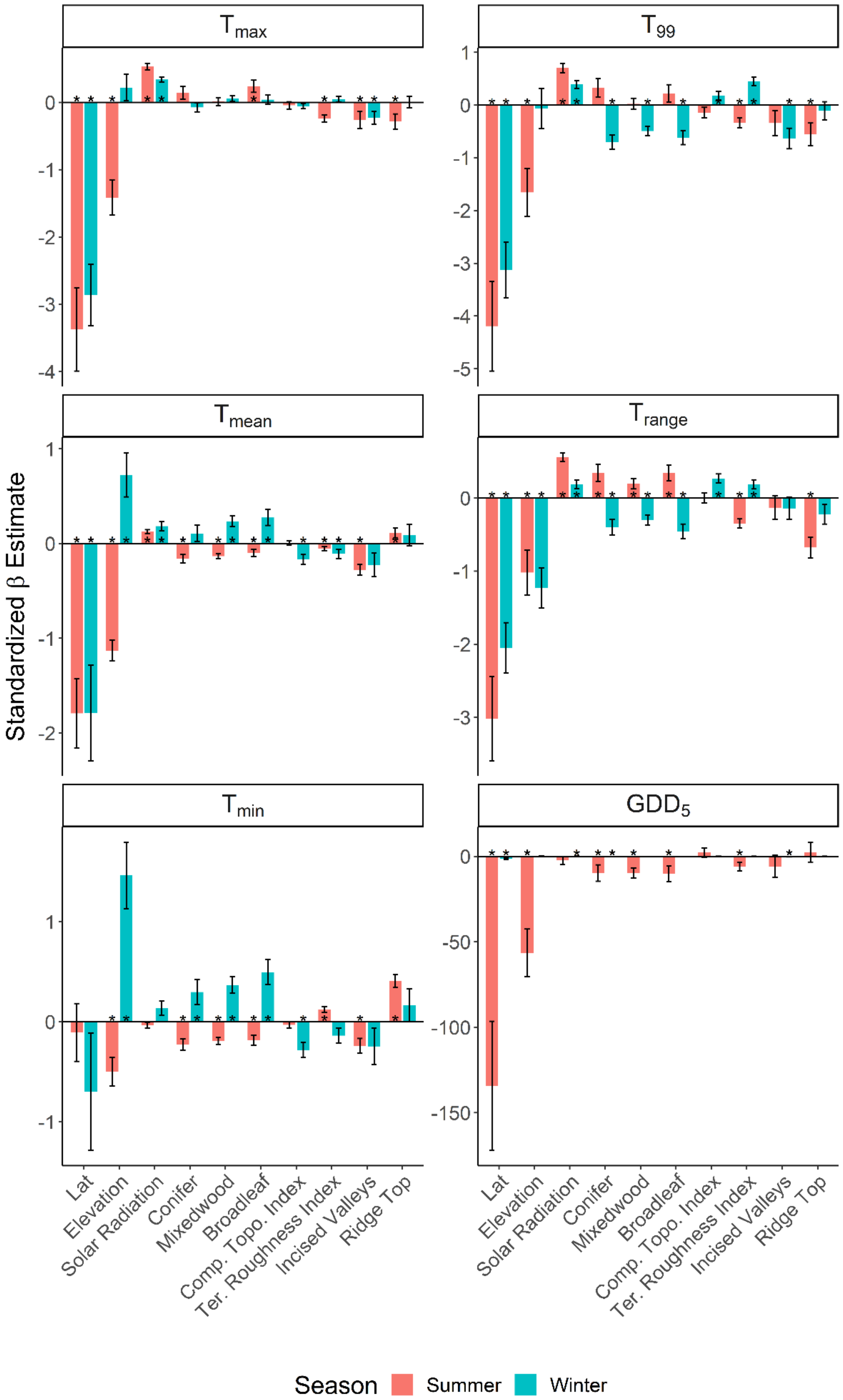


Figure S1.4: Standardized beta coefficients of all variables and temperature metrics of the full model for the summer and winter seasons over river valley and hill systems in Alberta, Canada. Error bars represent standard errors and * indicate

significant standardized estimates at $\alpha=0.05$. An explanation for each temperature metric can be found in the main text.

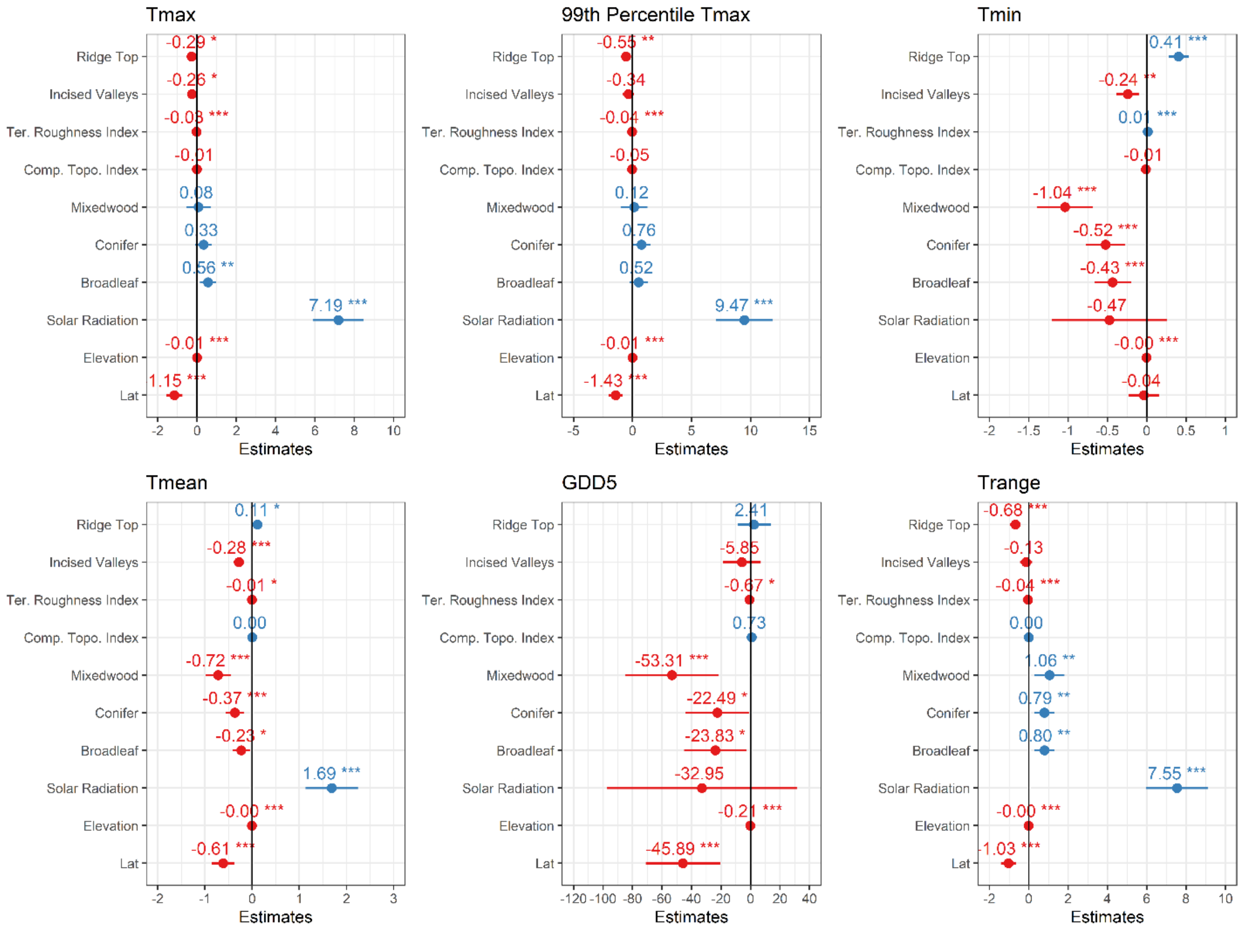


Figure S1.5: Unstandardized beta coefficients for topographic and vegetation cover effects on summer temperatures (2014-2020) at river valley and hill sites in Alberta, Canada. Refer to the main text for an explanation of each temperature metric. Bars indicate 95% confidence intervals with estimated coefficient on top of each line. Asterisks indicate significant estimates where the p-value is between 0 - 0.001 (‘*’), 0.001 - 0.01 (‘**’), and 0.01 - 0.05 (‘*’).**

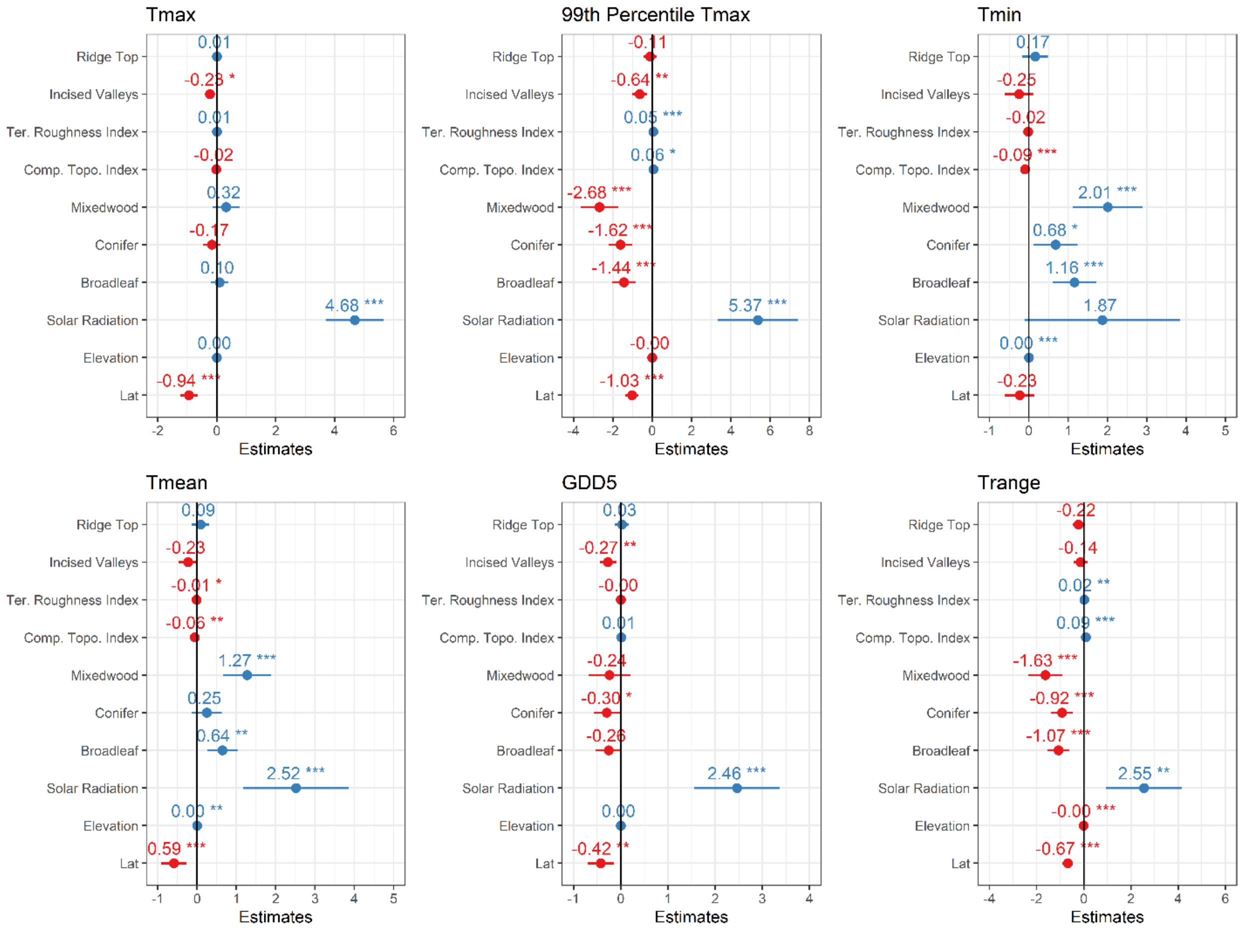


Figure S1.6: Unstandardized beta coefficients for topographic and vegetation cover effects on winter temperatures (2014-2020) at river valley and hill sites in Alberta, Canada. Refer to the main text for explanation of each temperature metric. Bars indicate 95% confidence intervals with estimated coefficient on top of each line. Asterisks indicate significant estimates where the p-value is between 0 - 0.001 (‘***’), 0.001 - 0.01 (‘**’), and 0.01 - 0.05 (‘*’).

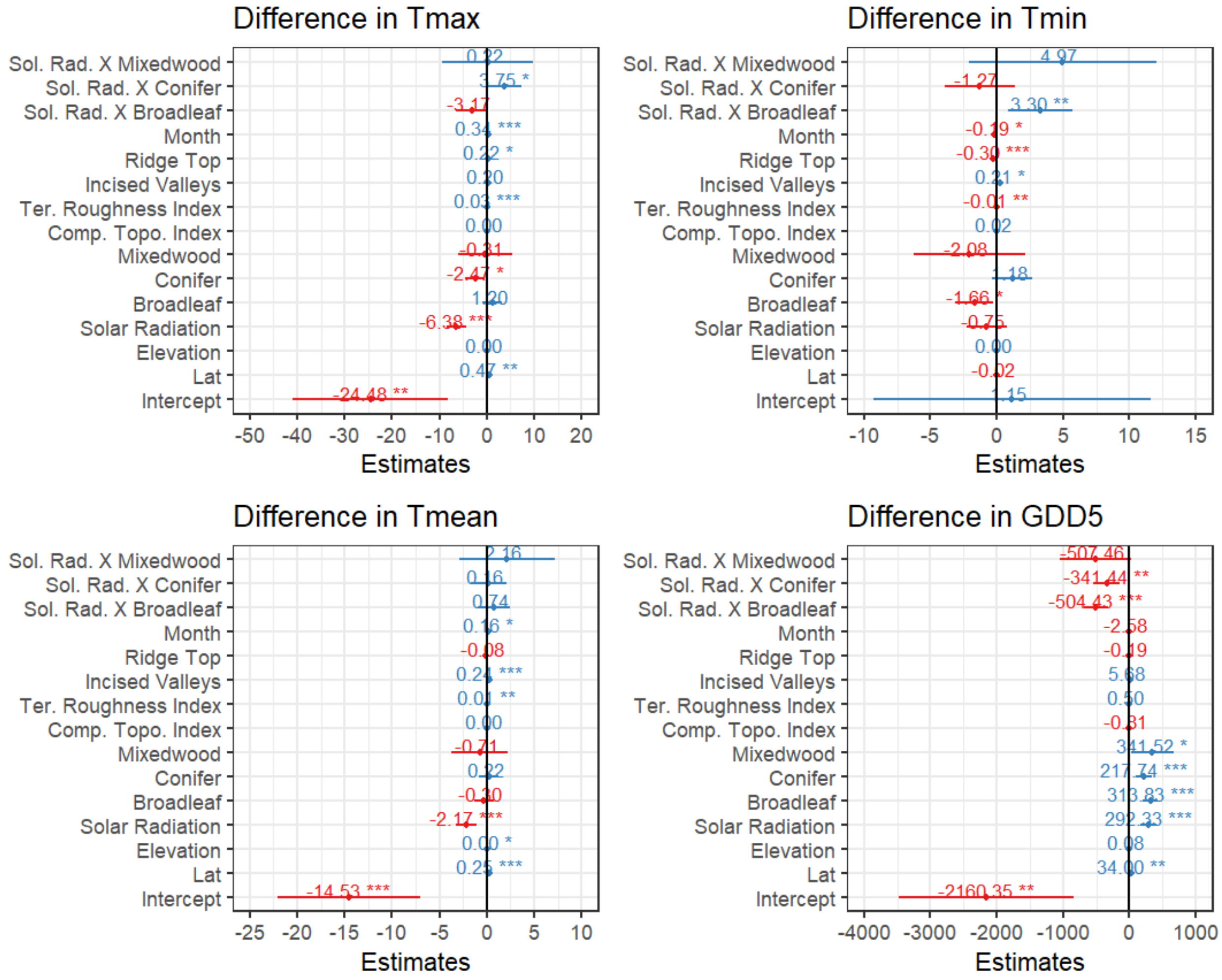


Figure S1.7: Unstandardized beta coefficients of different topographic variables and vegetation cover effects on the absolute difference between ClimateNA and iButton readings (i.e., $T_{Difference} = T_{ClimateNA}-T_{iButton}$) in different river valley and hill systems in Alberta, Canada during the summer 2014-2020. Refer to the main text for explanation of each temperature metric. Bars indicate 95% confidence intervals with estimated coefficient on top of each line. Asterisks indicate significant estimates where the p-value is between 0 - 0.001 (‘*’), 0.001 - 0.01 (‘**’), and 0.01 - 0.05 (‘*’).**

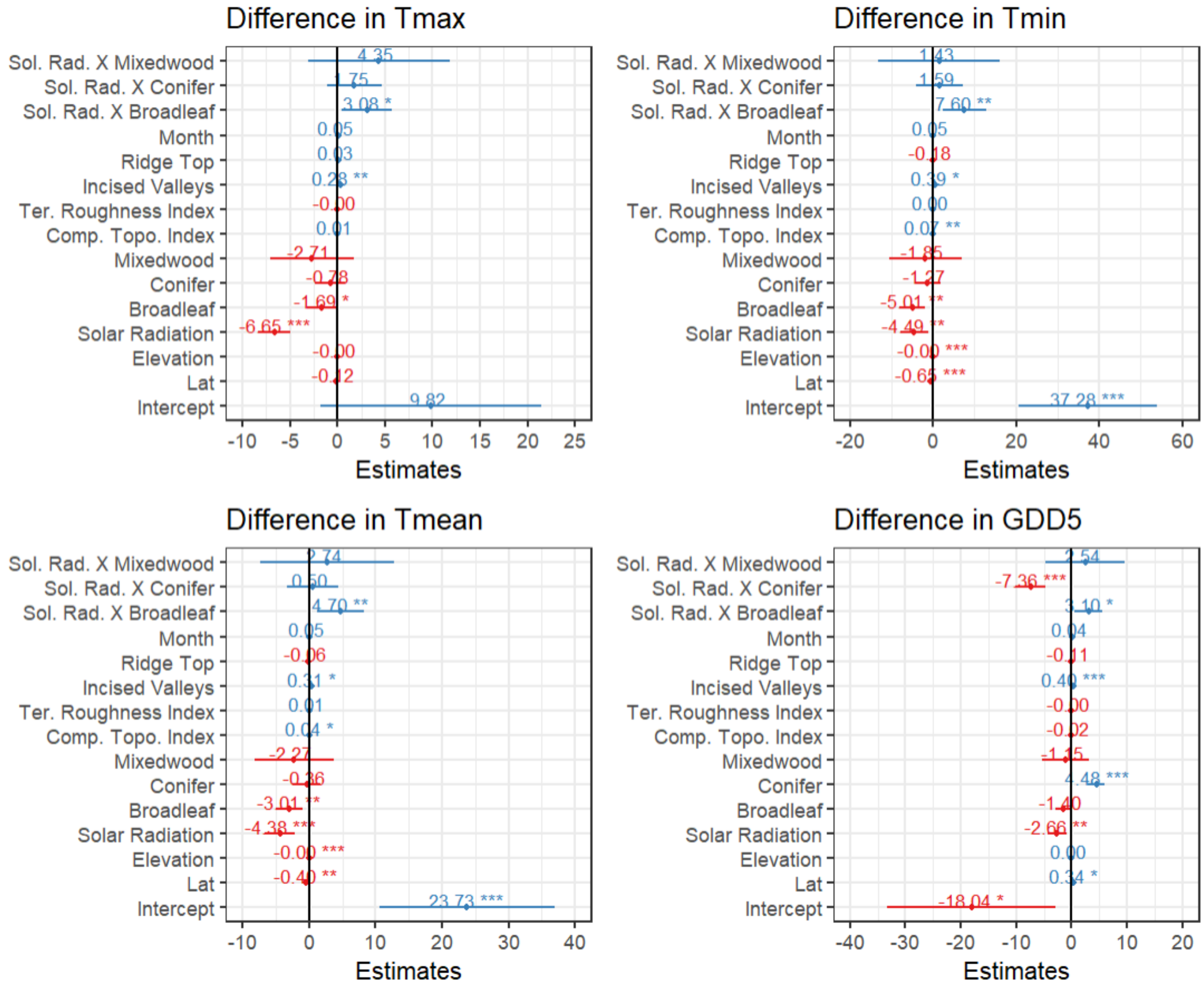


Figure S1.8: Unstandardized beta coefficients of different topographic variables and vegetation cover effects on the absolute difference between ClimateNA and iButton readings (i.e., $T_{Difference} = T_{ClimateNA}-T_{iButton}$) in different river valley and hill systems in Alberta, Canada during the winter 2014-2020. Refer to the main text for explanation of each temperature metrics. Bars indicate 95% confidence intervals with estimated

coefficient on top of each line. Asterisks indicate significant estimates where the p-value is between 0 - 0.001 (‘*’), 0.001 - 0.01 (‘**’), and 0.01 - 0.05 (‘*’).**

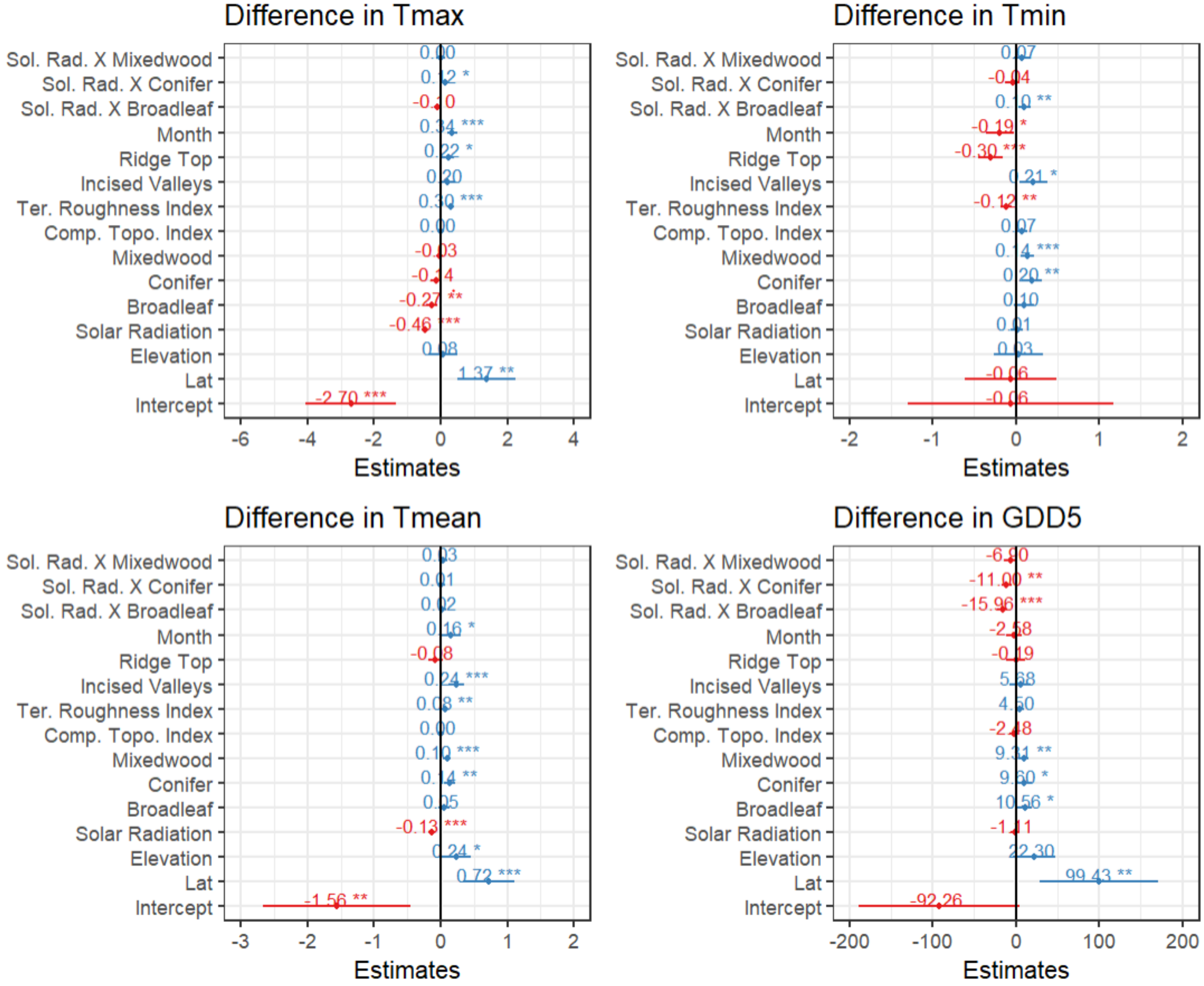


Figure S1.9: Standardized beta coefficients of different topographic variables and vegetation cover effects on the absolute difference between ClimateNA and iButton readings (i.e., $T_{Difference} = T_{ClimateNA} - T_{iButton}$) in different river valley and hill systems in Alberta, Canada during the summer 2014-2020. Refer to the main text for explanation of each temperature metrics. Bars indicate 95% confidence intervals with estimated

coefficient on top of each line. Asterisks indicate significant estimates where the p-value is between 0 - 0.001 (‘*’), 0.001 - 0.01 (‘**’), and 0.01 - 0.05 (‘*’).**

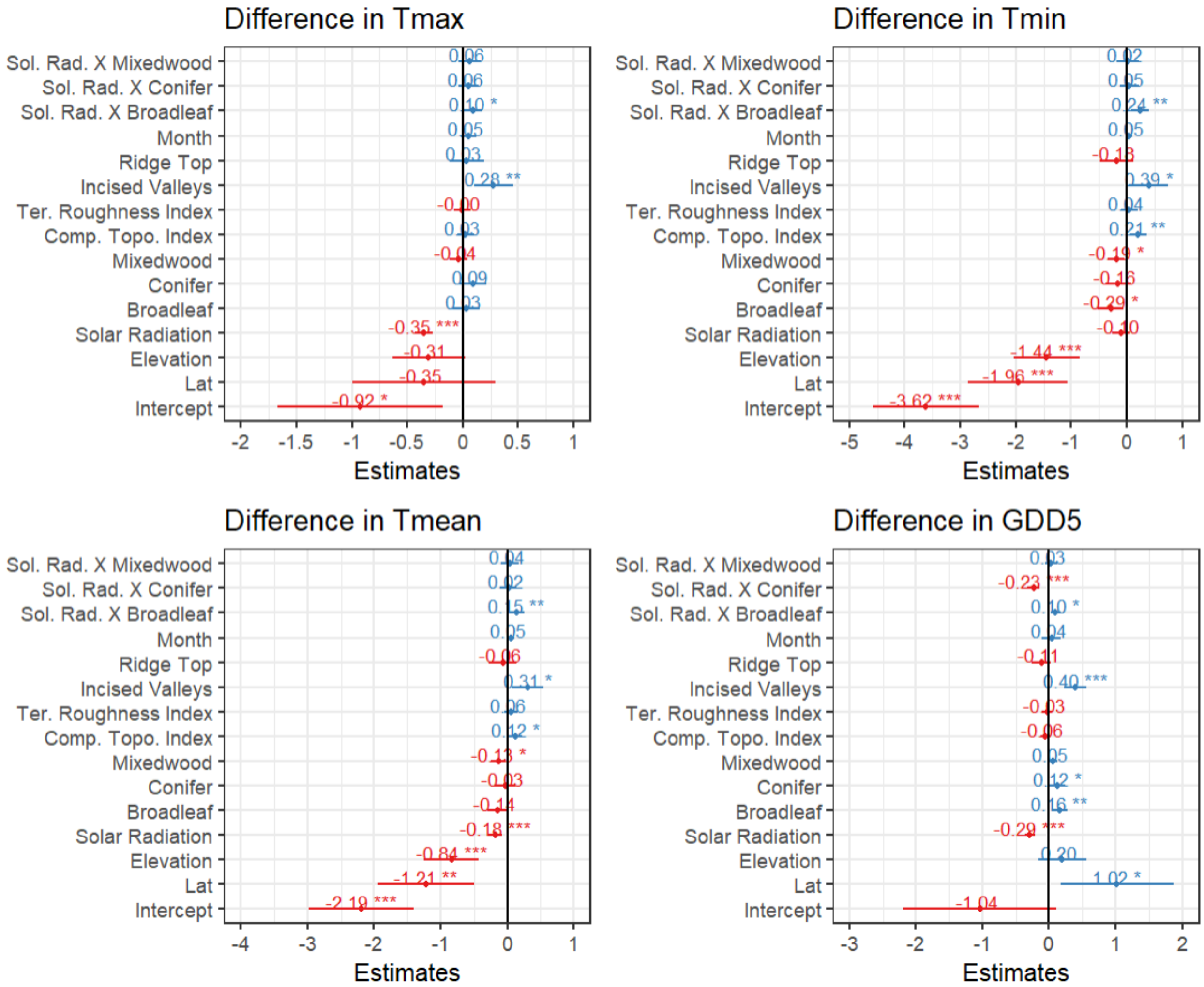


Figure S1.10: Standardized beta coefficients of different topographic variables and vegetation cover effects on the absolute difference between ClimateNA and iButton readings (i.e., $T_{Difference} = T_{ClimateNA}-T_{iButton}$) in different river valley and hill systems in Alberta, Canada during the winter 2014-2020. Refer to the main text for explanation of each temperature metrics. Bars indicate 95% confidence intervals with estimated coefficient on top of each line. Asterisks indicate significant estimates where the p-value is between 0 - 0.001 (‘***’), 0.001 - 0.01 (‘**’), and 0.01 - 0.05 (‘*’).

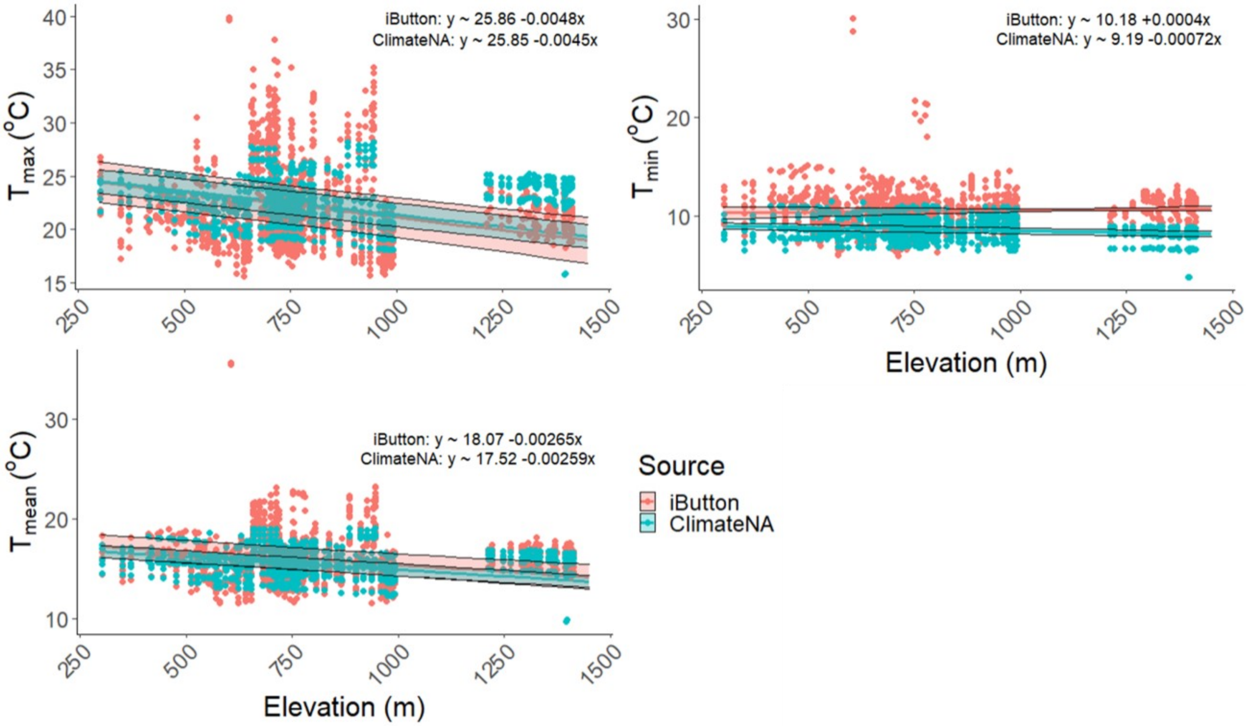


Figure S1.11: The effect of elevation over ClimateNA and iButton readings monthly average of daily maxima **(T_{max}), minima (T_{min}) and mean (T_{mean}) in different river valley and**

hill systems in Alberta, Canada during the summer months of 2014-2020. Different sources of data are plotted with different colors.

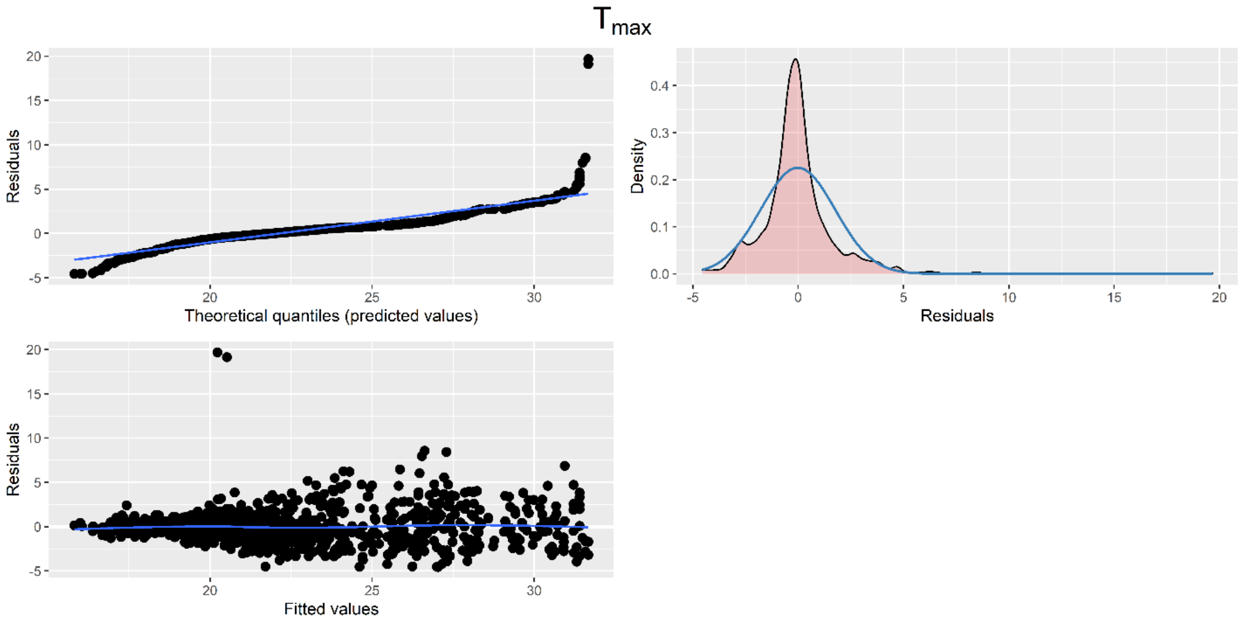


Figure S1.12: Model diagnostics for the monthly average of the daily maximum temperature **for the *summer* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.**

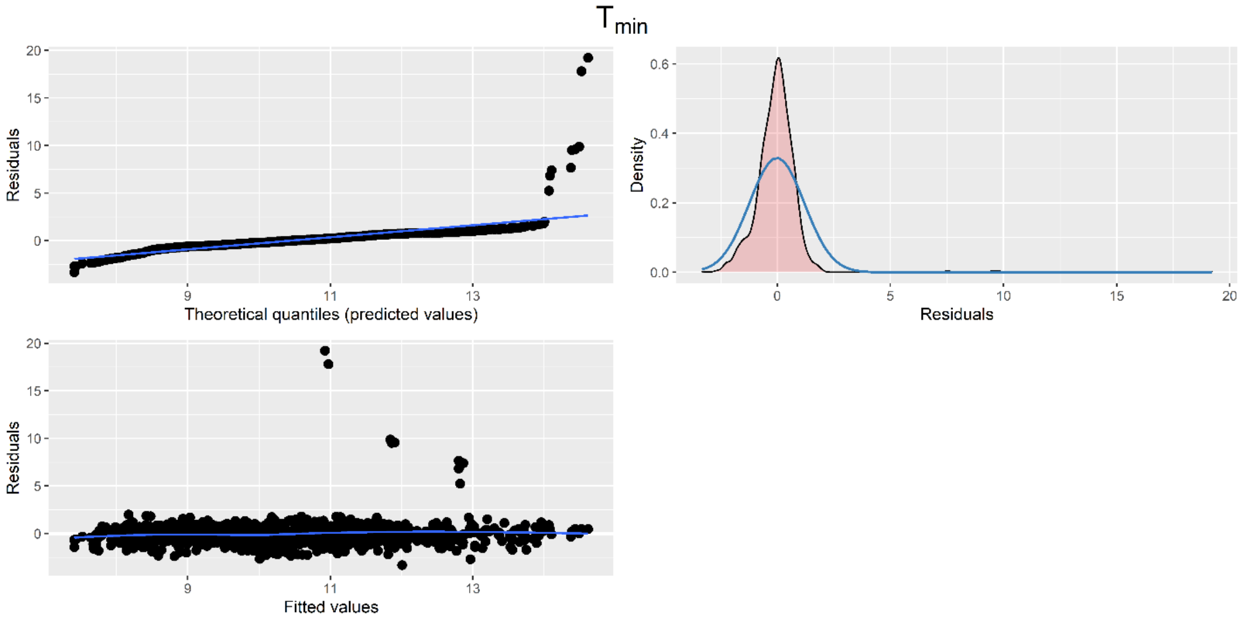


Figure S1.13: Model diagnostics for the monthly average of the daily minimum temperature for the *summer* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

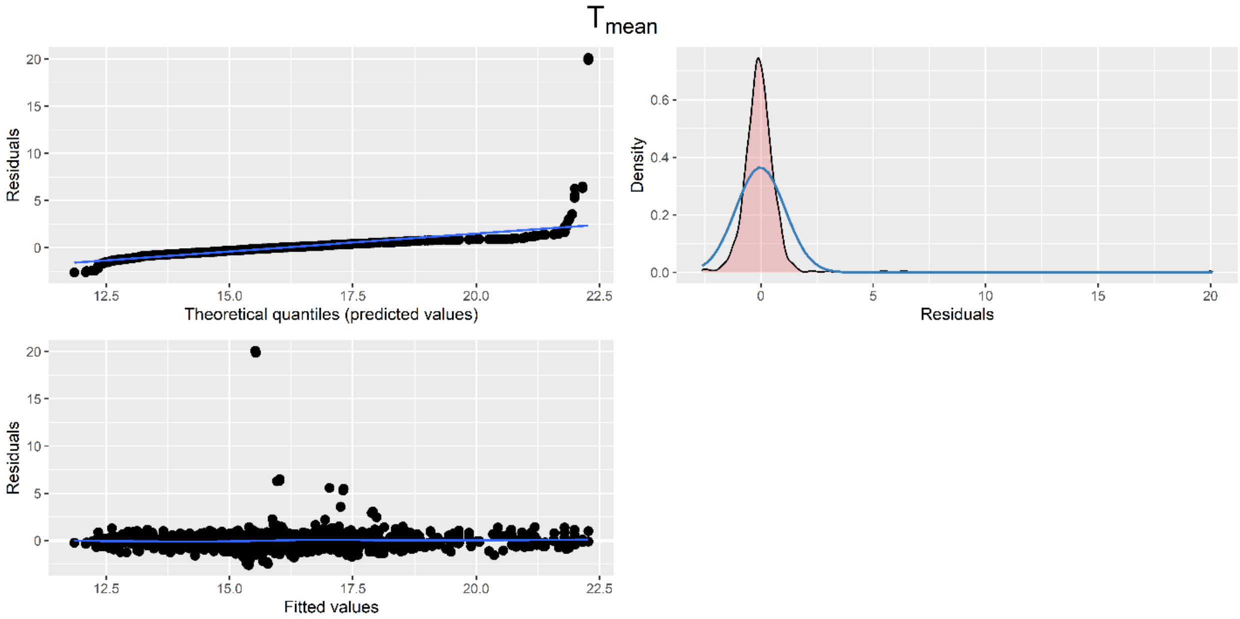


Figure S1.14: Model diagnostics for the monthly average of the daily mean temperature for the *summer* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

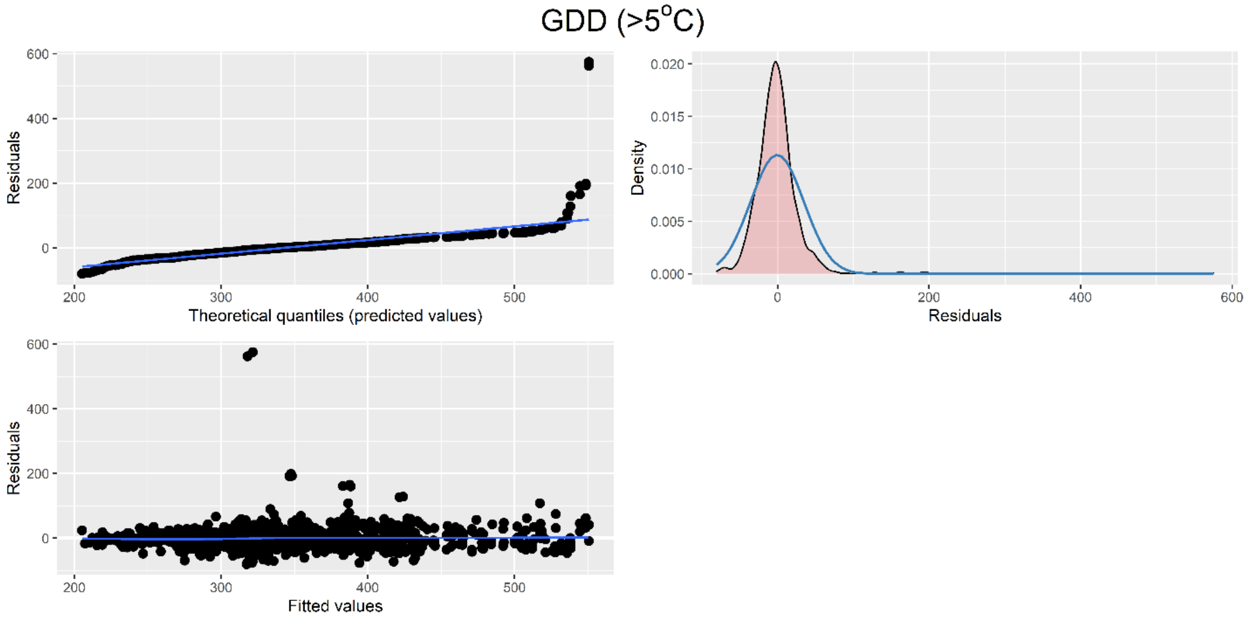


Figure S1.15: Model diagnostics for the monthly average growing degree days above 5 ˚C for the *summer* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

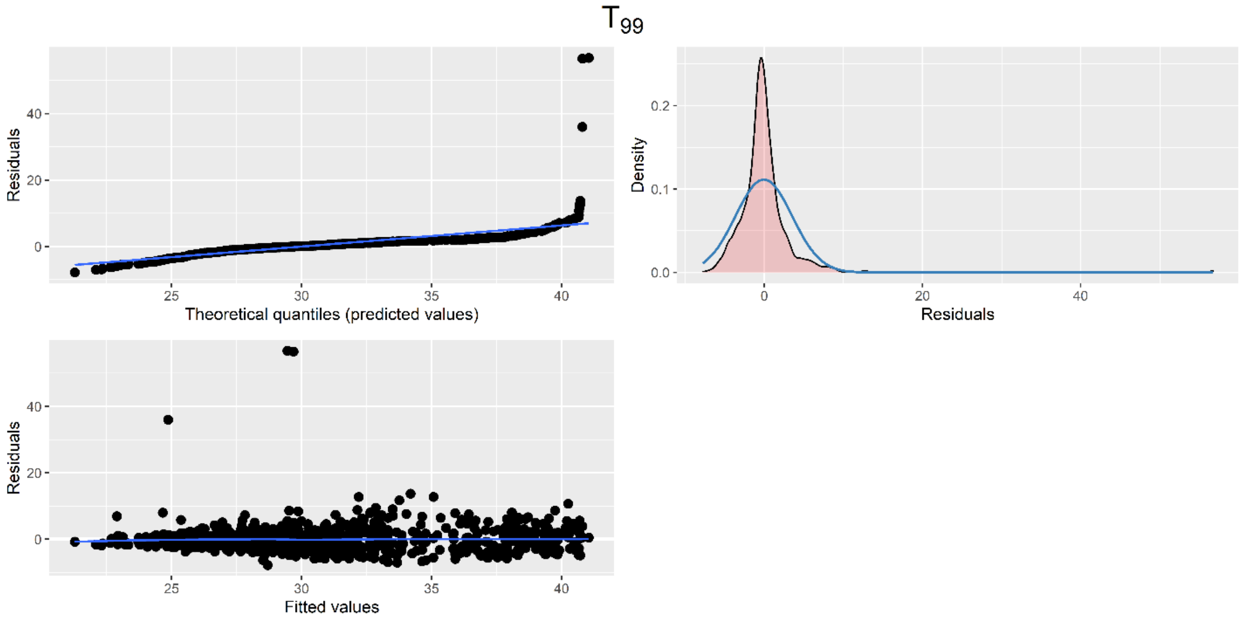


Figure S1.16: Model diagnostics for the 99th percentile of daily maxima for the *summer* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

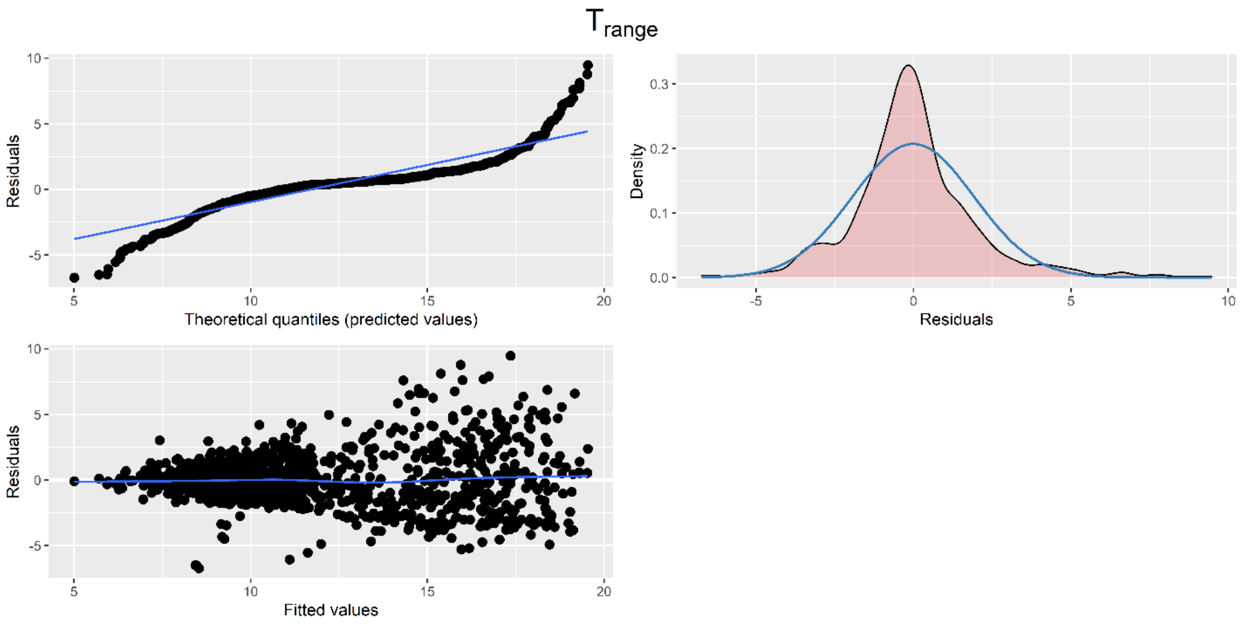


Figure S1.17: Model diagnostics for the monthly average of daily temperature range for the *summer* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

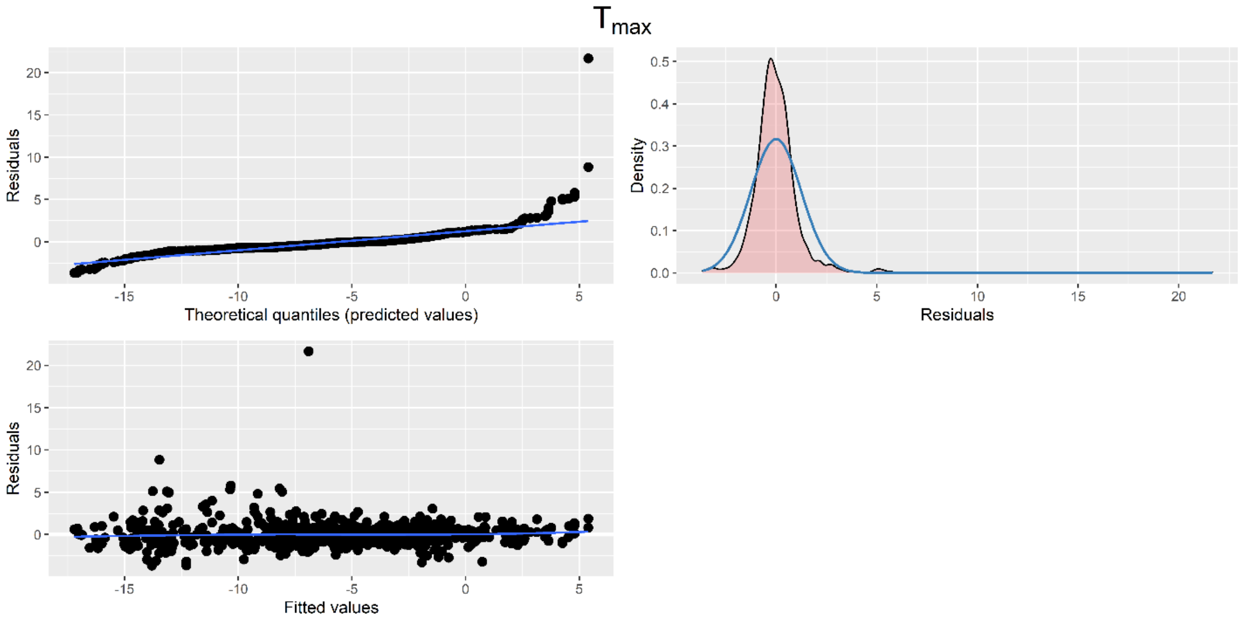


Figure S1.18: Model diagnostics for the monthly average of the daily maximum temperature for the *winter* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

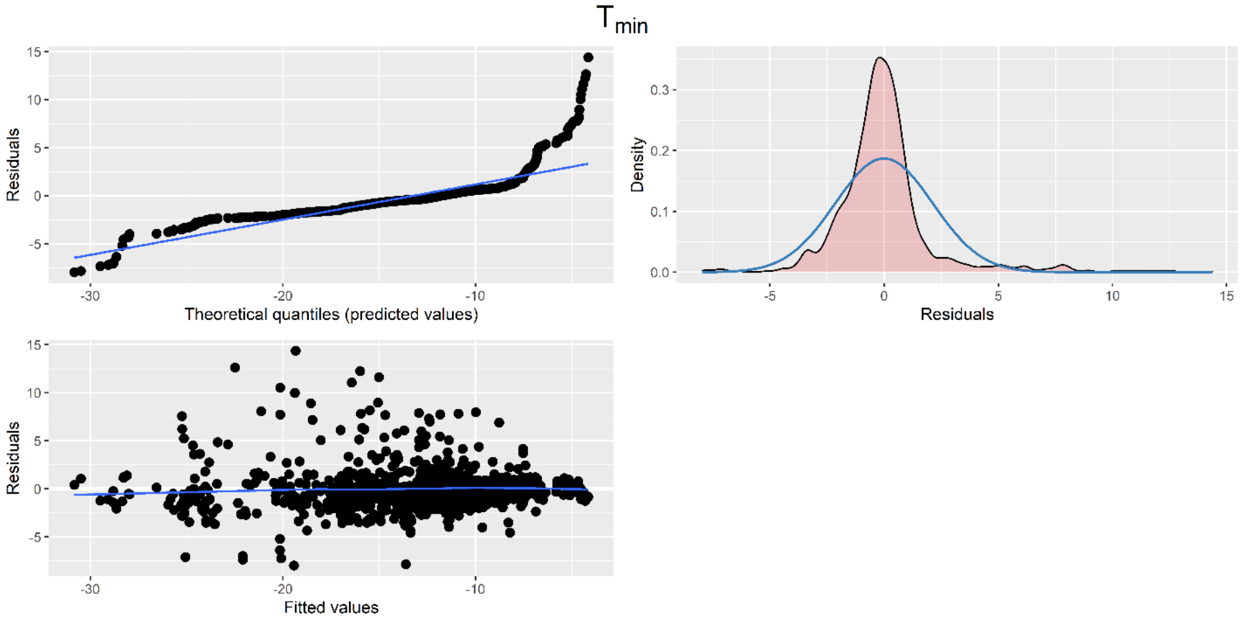


Figure S1.19: Model diagnostics for the monthly average of the daily minimum temperature for the *winter* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

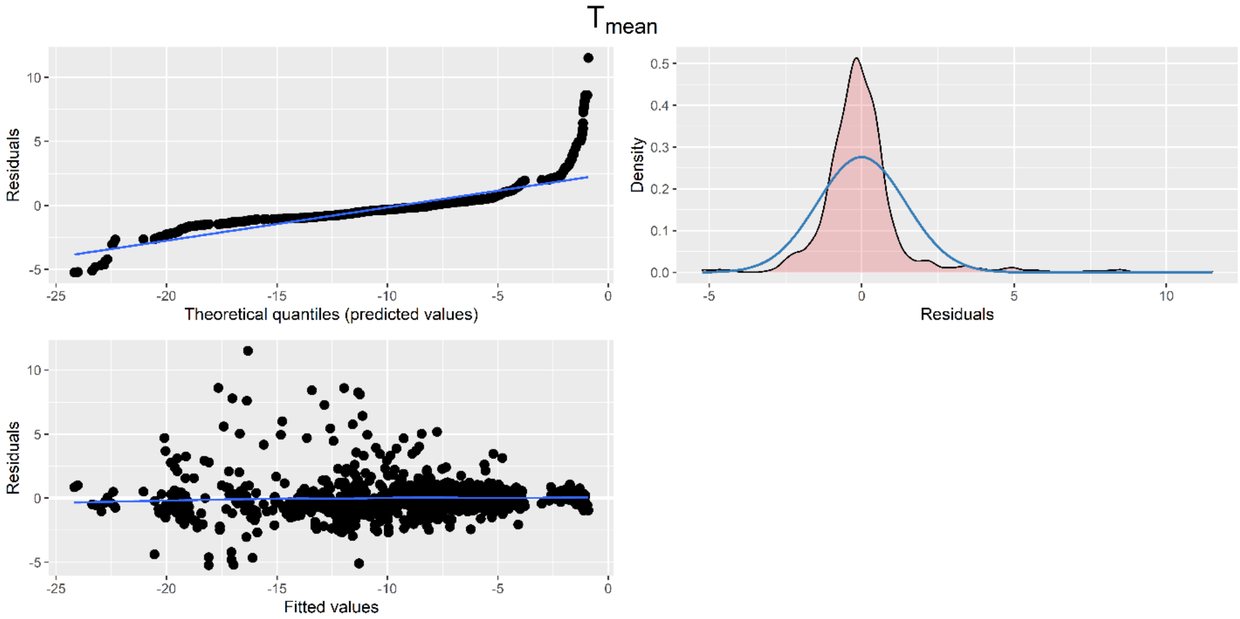


Figure S1.20: Model diagnostics for the monthly average of the daily mean temperature for the *winter* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

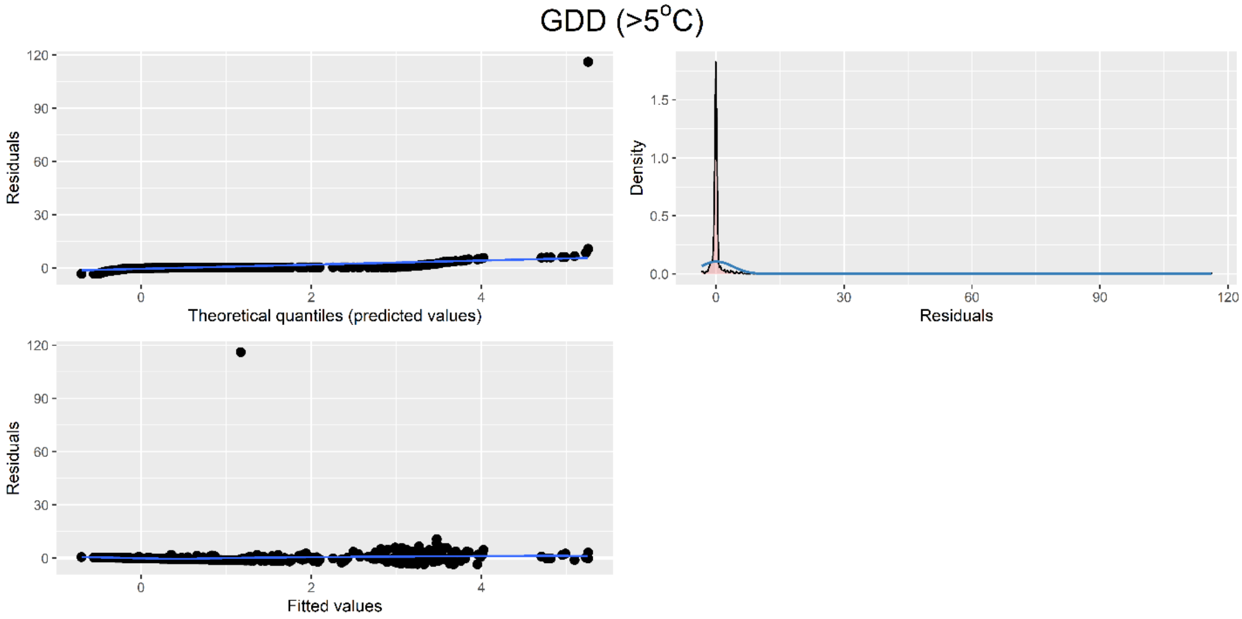


Figure S1.21: Model diagnostics for the monthly average growing degree days above 5 ˚C for the *winter* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

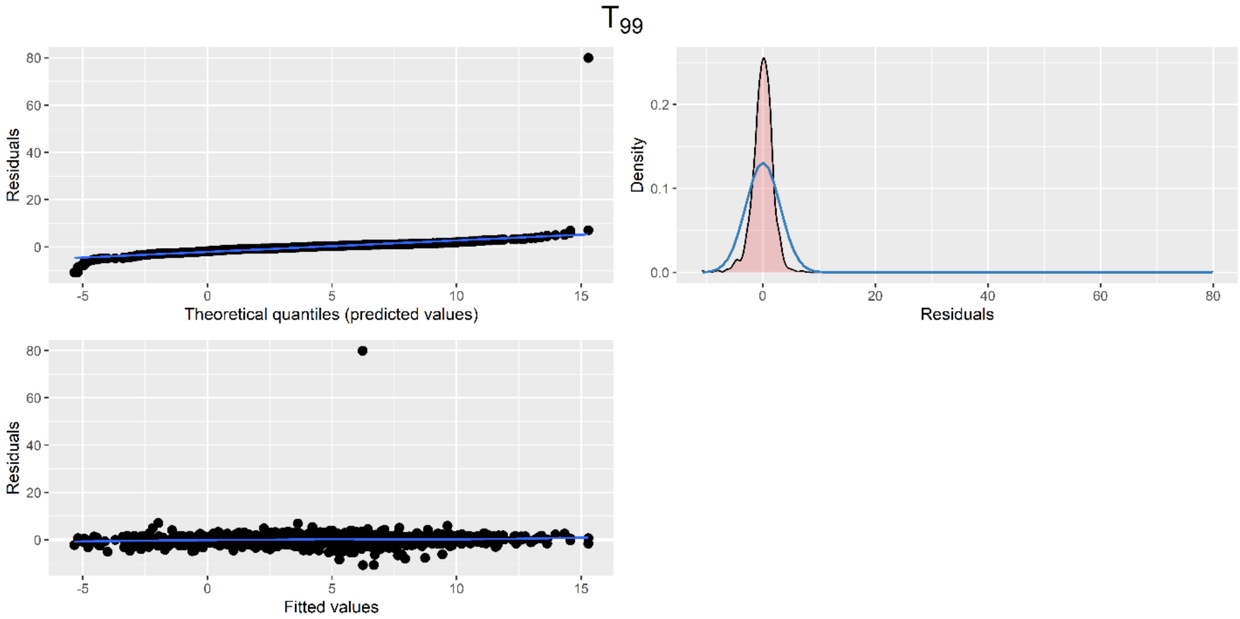


Figure S22: Model diagnostics for the 99th percentile of daily maxima for the *winter* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

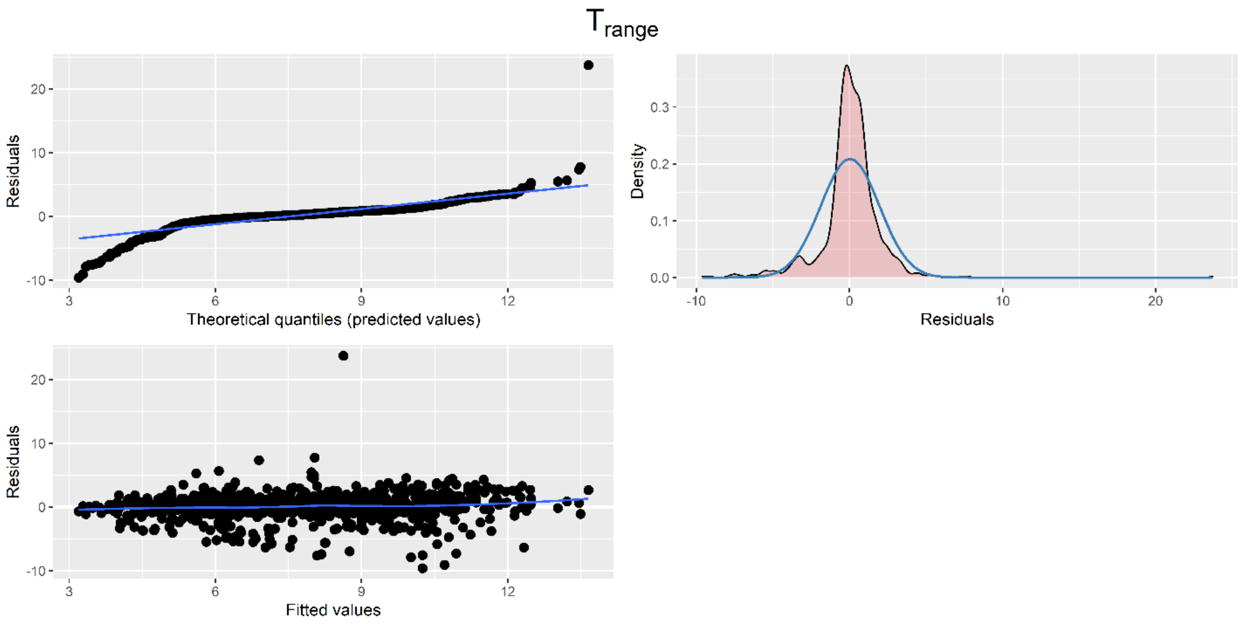


Figure S1.22: Model diagnostics for the monthly average of daily temperature range for the *winter* season. Residuals are for the *full model* with *scaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

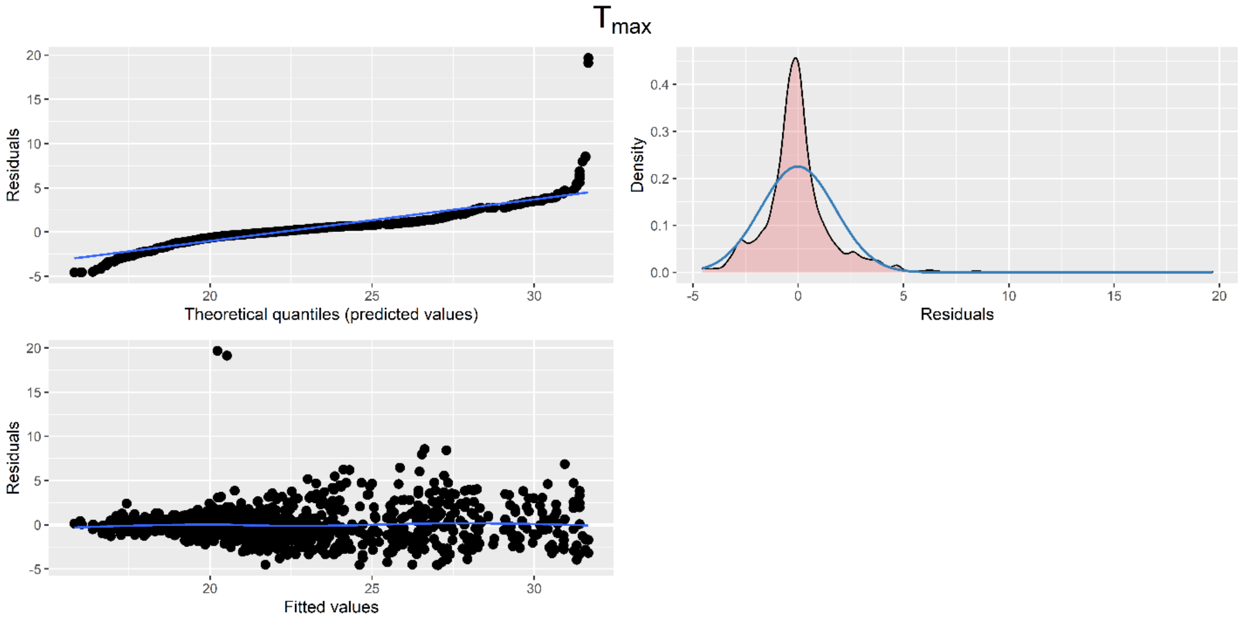


Figure S1.23: Model diagnostics for the monthly average of the daily maximum temperature for the *summer* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

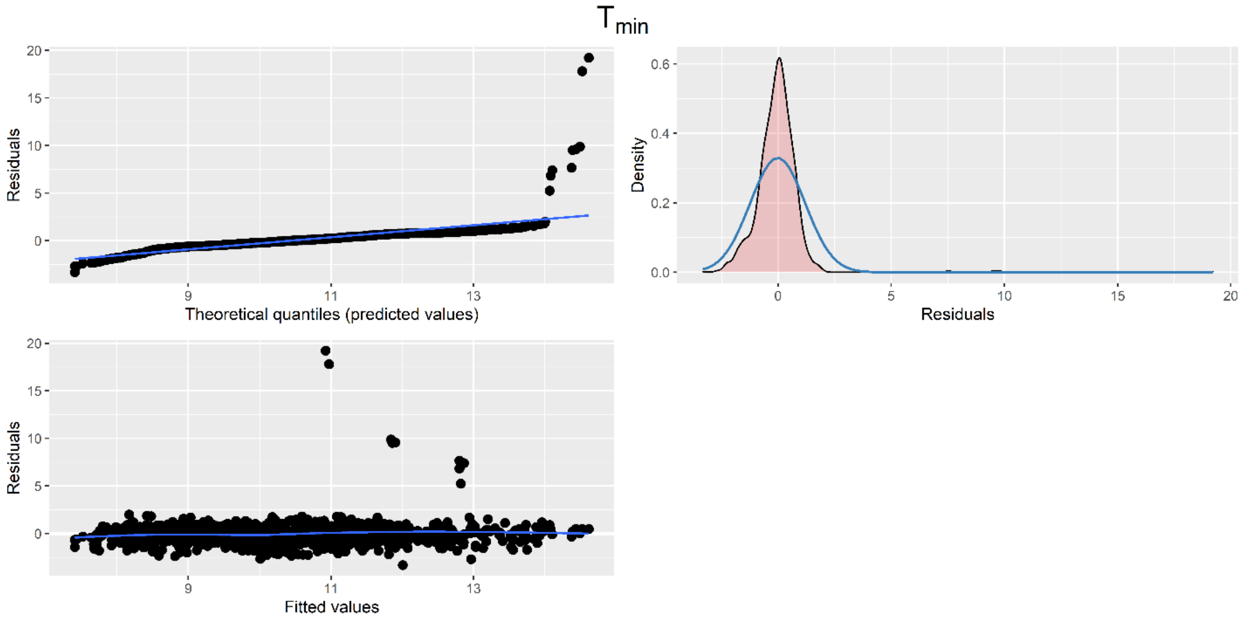


Figure S1.24: Model diagnostics for the monthly average of the daily minimum temperature for the *summer* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

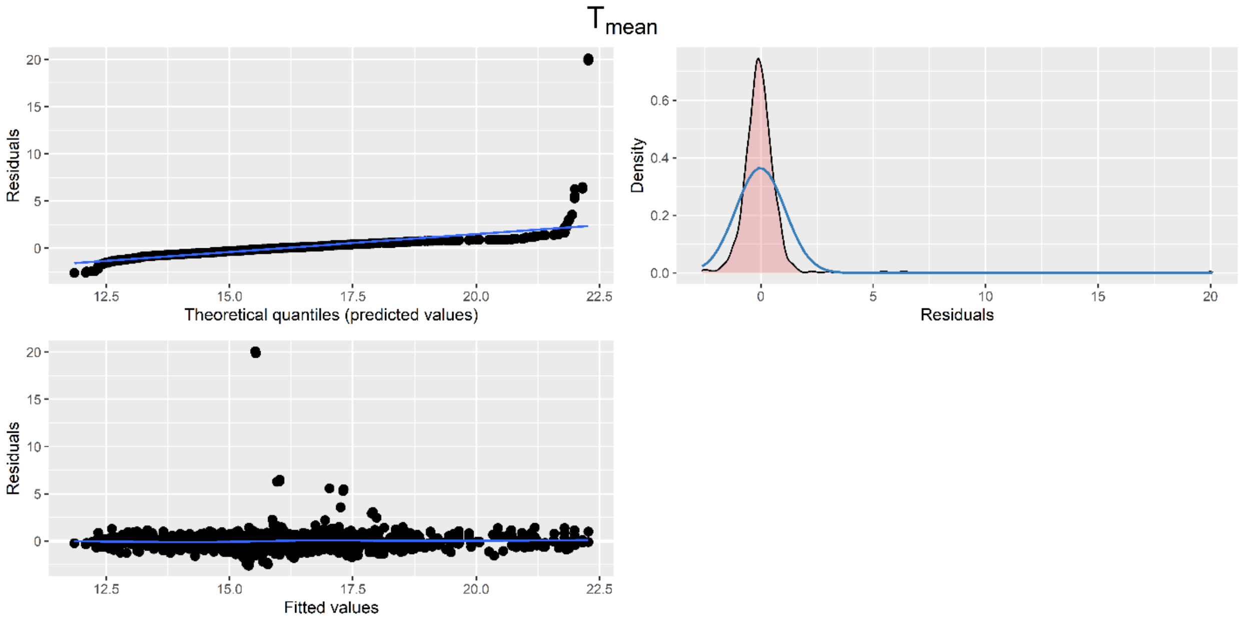


Figure S1.25: Model diagnostics for the monthly average of the daily mean temperature for the *summer* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

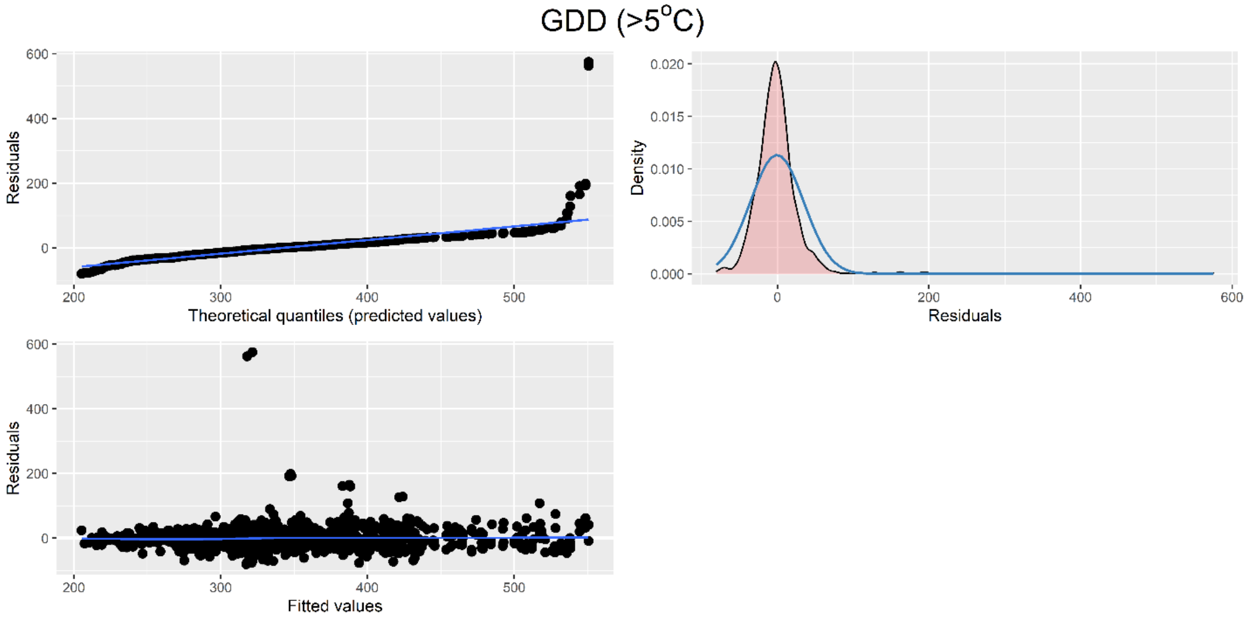


Figure S1.26: Model diagnostics for the monthly average growing degree days above 5 ˚C for the *summer* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

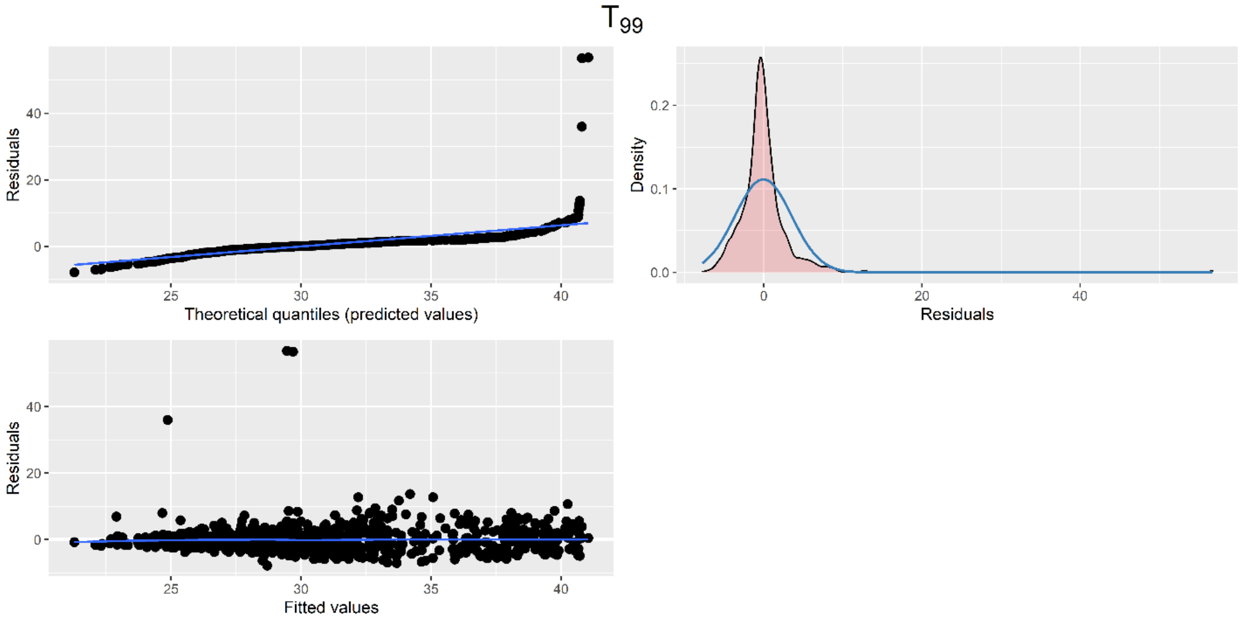


Figure S1.27: Model diagnostics for the 99th percentile of daily maxima for the *summer* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

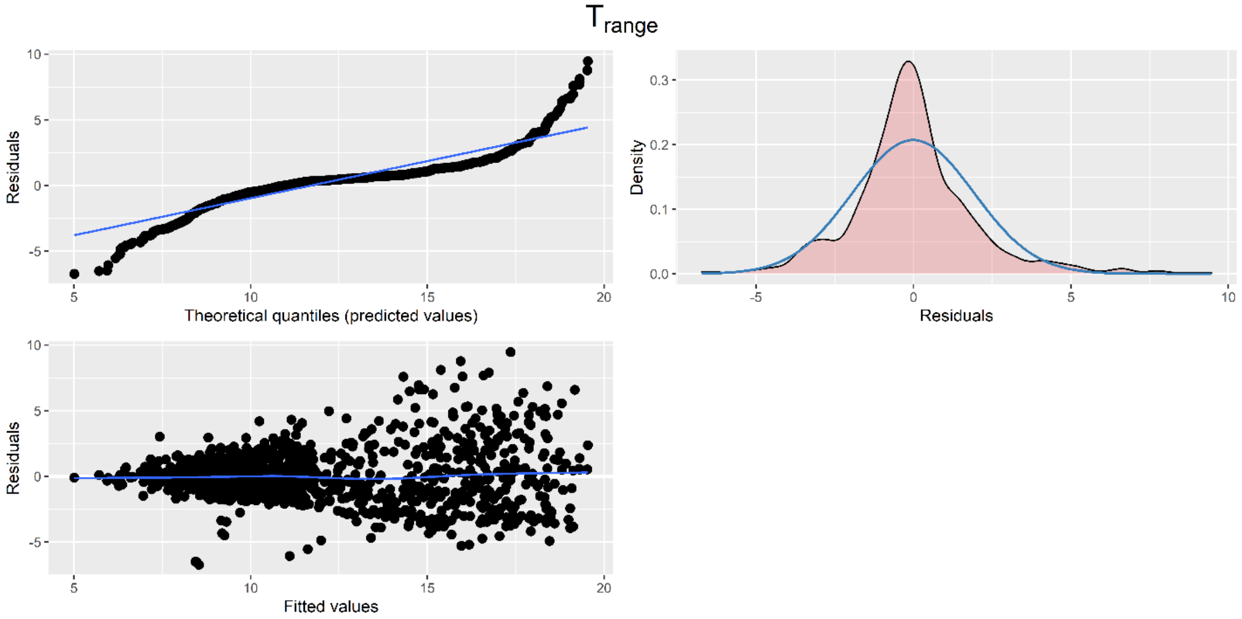


Figure S1.28: Model diagnostics for the monthly average of daily temperature range for the *summer* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

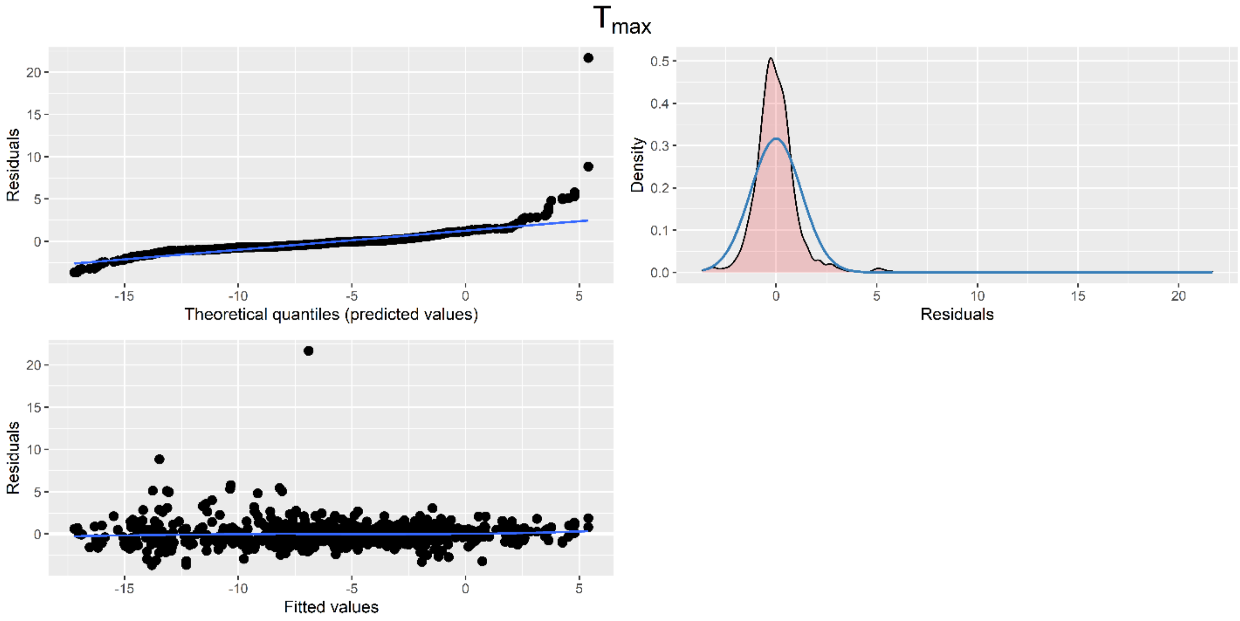


Figure S1.29: Model diagnostics for the monthly average of the daily maximum temperature for the *winter* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

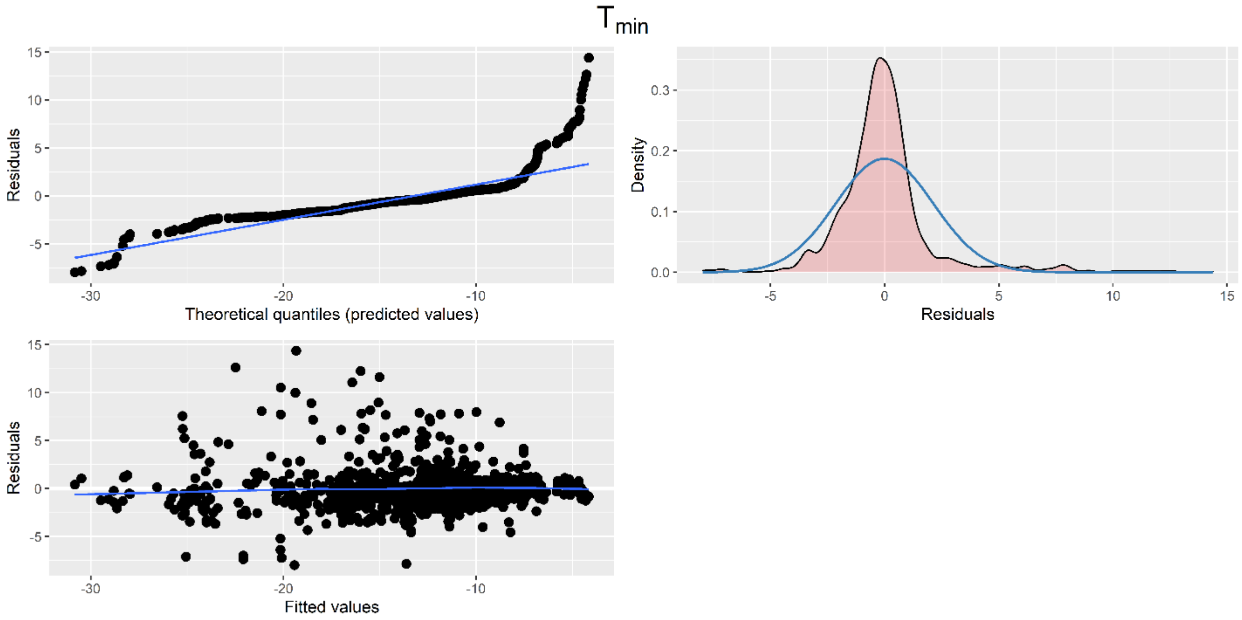


Figure S1.30: Model diagnostics for the monthly average of the daily minimum temperature for the *winter* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

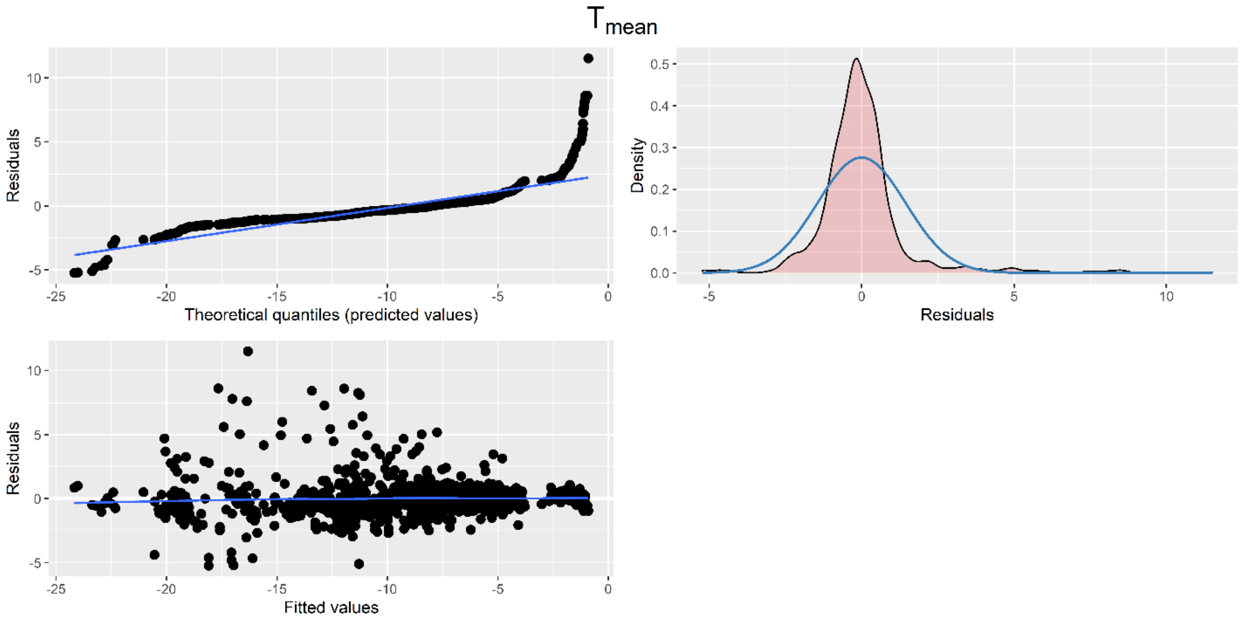


Figure S1.31: Model diagnostics for the monthly average of the daily mean temperature for the *winter* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

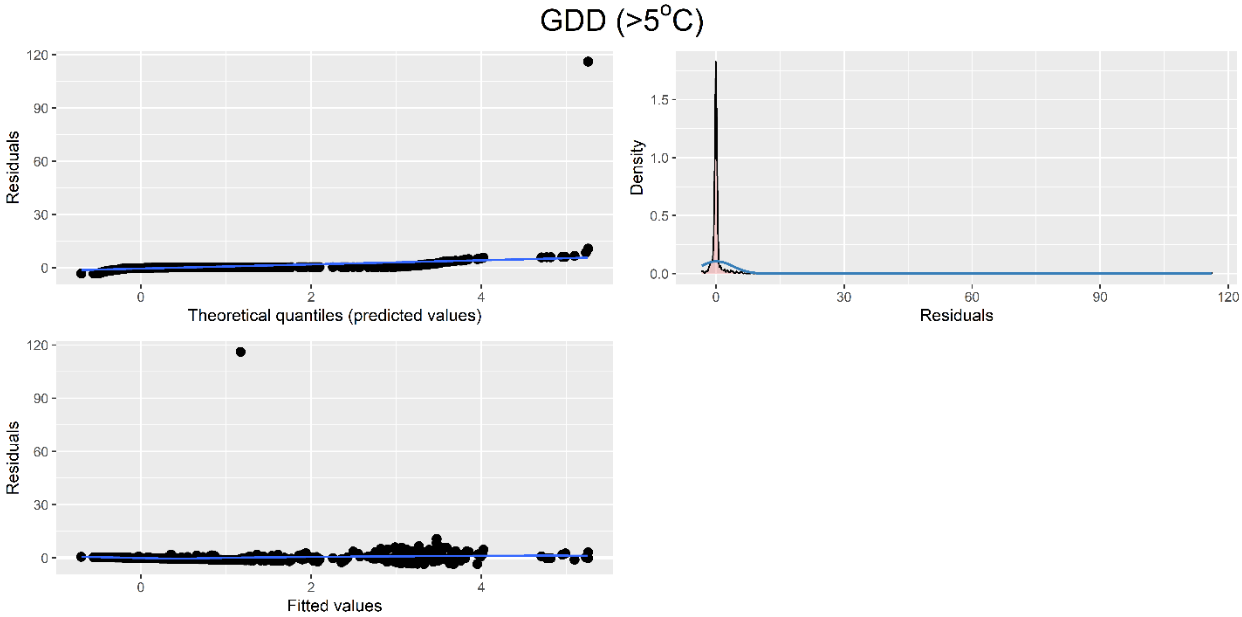


Figure S1.32: Model diagnostics for the monthly average growing degree days above 5 ˚C for the *winter* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

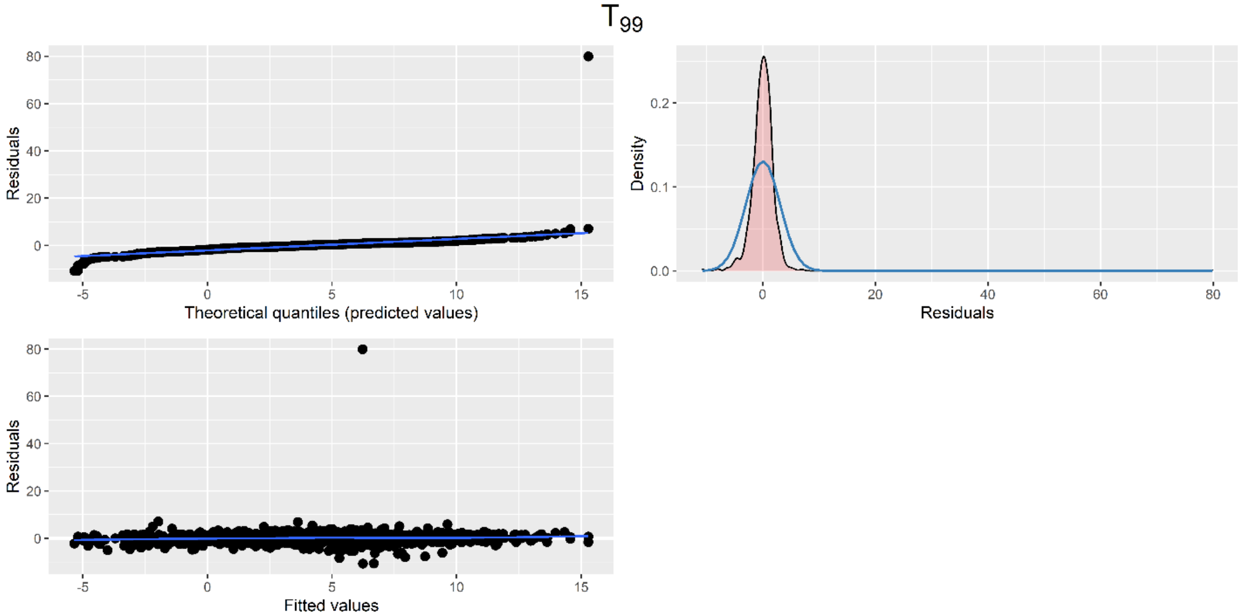


Figure S1.33: Model diagnostics for the 99th percentile of daily maxima for the *winter* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

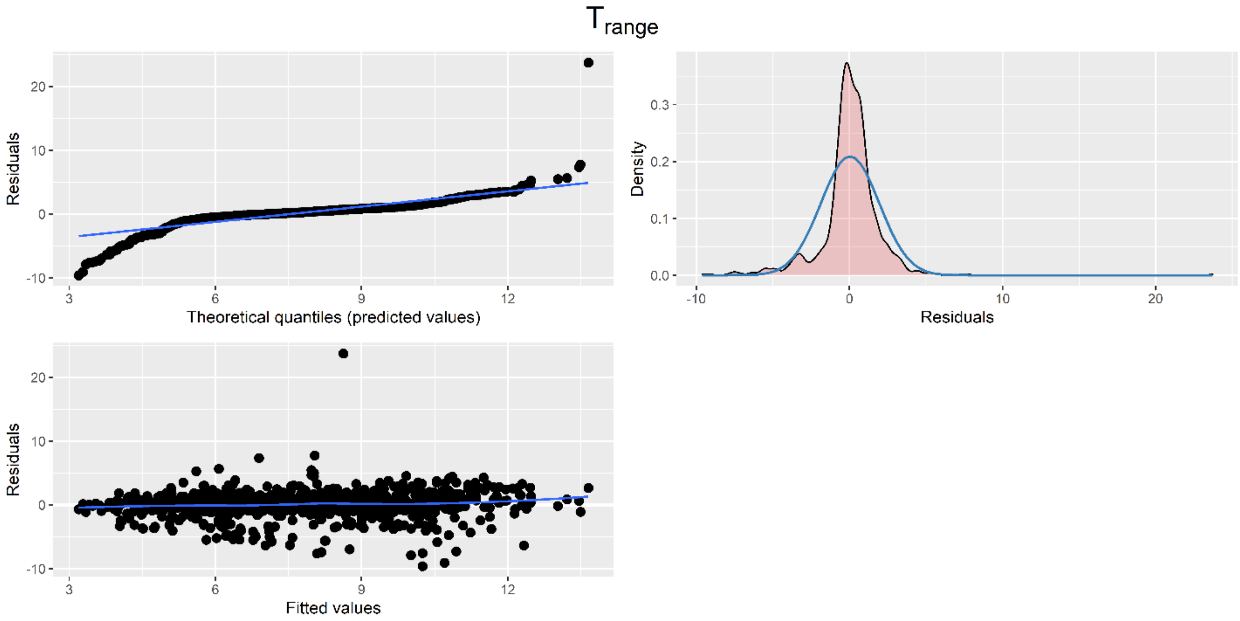


Figure S1.34: Model diagnostics for the monthly average of daily temperature range for the *winter* season. Residuals are for the *full model* with *unscaled* variables. Please refer to the Methods section in the main text for an explanation of each metric.

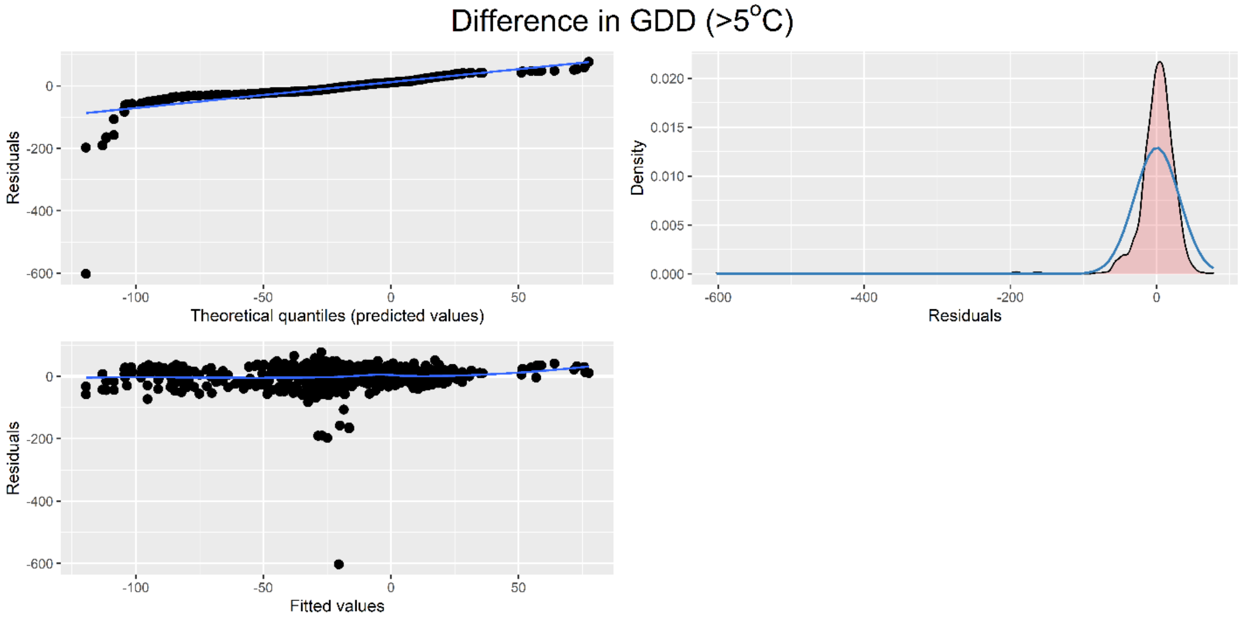


Figure S1.35: Model diagnostics for the absolute difference in monthly average growing degree days above 5 ˚C between ClimateNA and iButton readings ($T_{Difference}$ = $T_{ClimateNA}$ - $T_{iButton}$) for the *summer* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *scaled* variables.

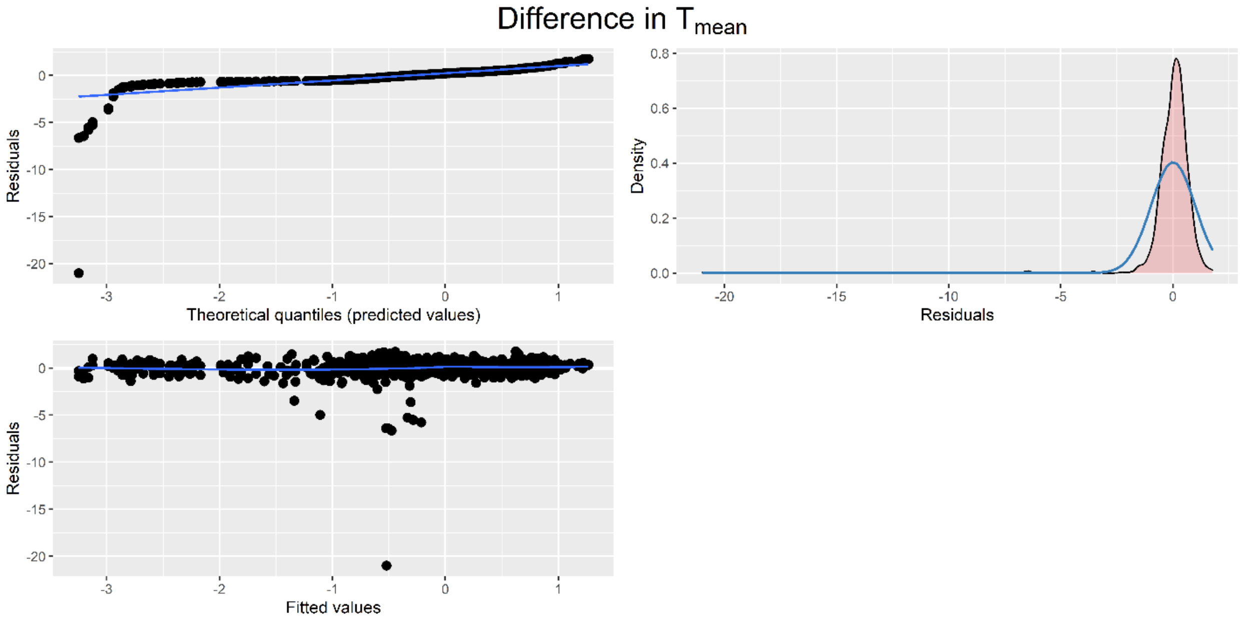


Figure S1.36: Model diagnostics for the absolute difference in monthly average of the daily mean temperature between ClimateNA and iButton readings ($T_{Difference} = T_{ClimateNA} - T_{iButton}$) for the *summer* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *scaled* variables.

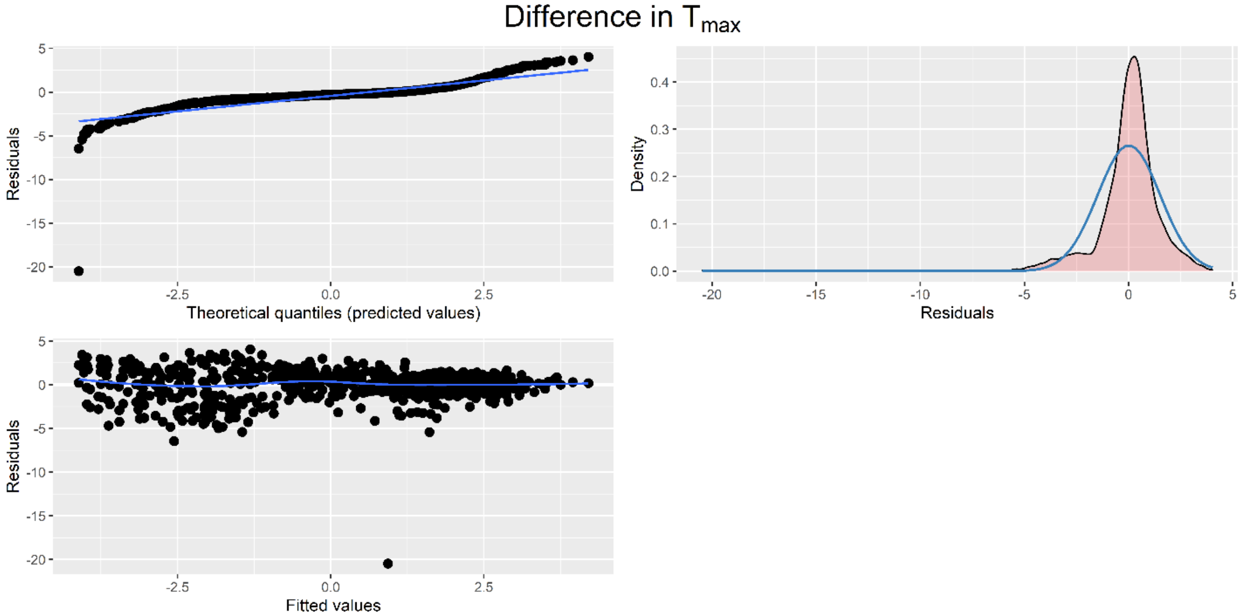


Figure S1.37: Model diagnostics for the absolute difference in monthly average of the daily maxima temperature between ClimateNA and iButton readings ($T_{Difference}$ = $T_{ClimateNA}$ - $T_{iButton}$) for the *summer* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *scaled* variables.

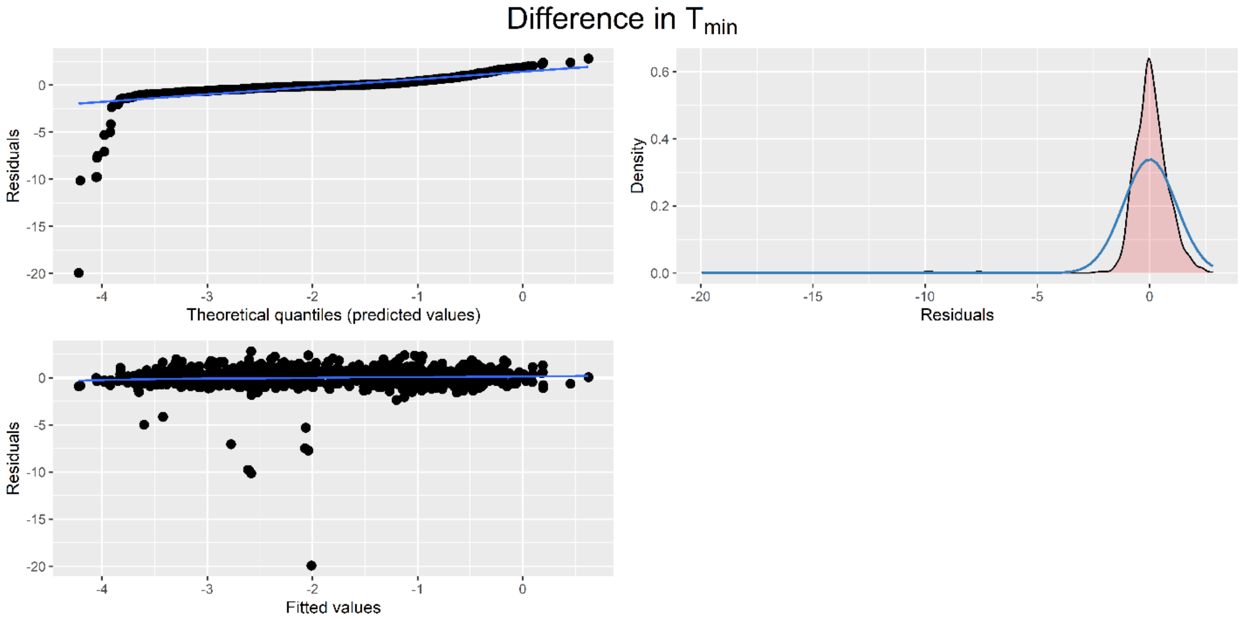


Figure S1.38: Model diagnostics for the absolute difference in monthly average of the daily minimum temperature between ClimateNA and iButton readings ($T_{Difference} = T_{ClimateNA} - T_{iButton}$) for the *summer* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *scaled* variables.

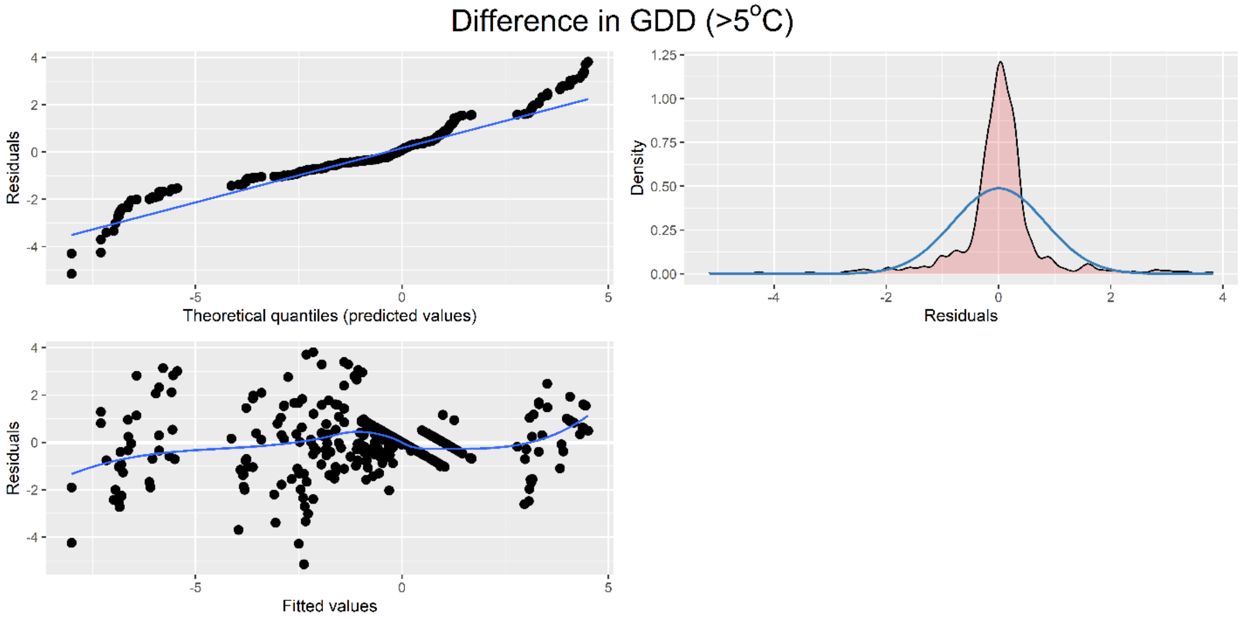


Figure S1.39: Model diagnostics for the absolute difference in monthly average growing degree days above 5 ˚C between ClimateNA and iButton readings ($T_{Difference}$ = $T_{ClimateNA}$ - $T_{iButton}$) for the *winter* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *scaled* variables.

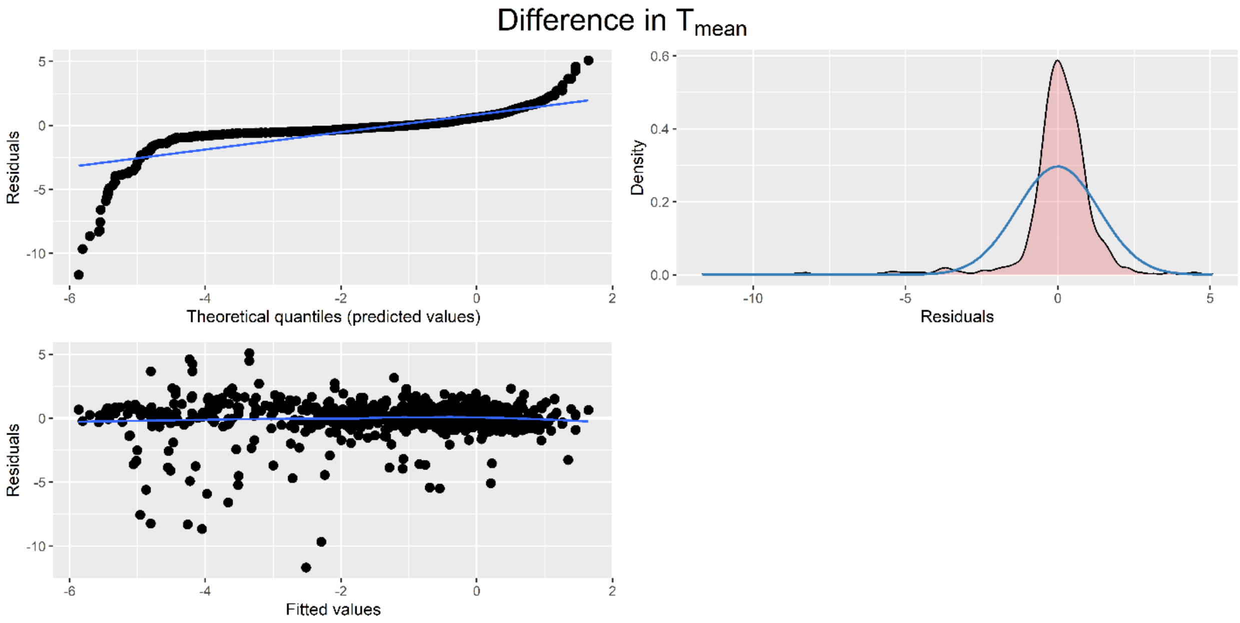


Figure S1.40: Model diagnostics for the absolute difference in monthly average of the daily mean temperature between ClimateNA and iButton readings ($T_{Difference} = T_{ClimateNA} - T_{iButton}$) for the *winter* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *scaled* variables.

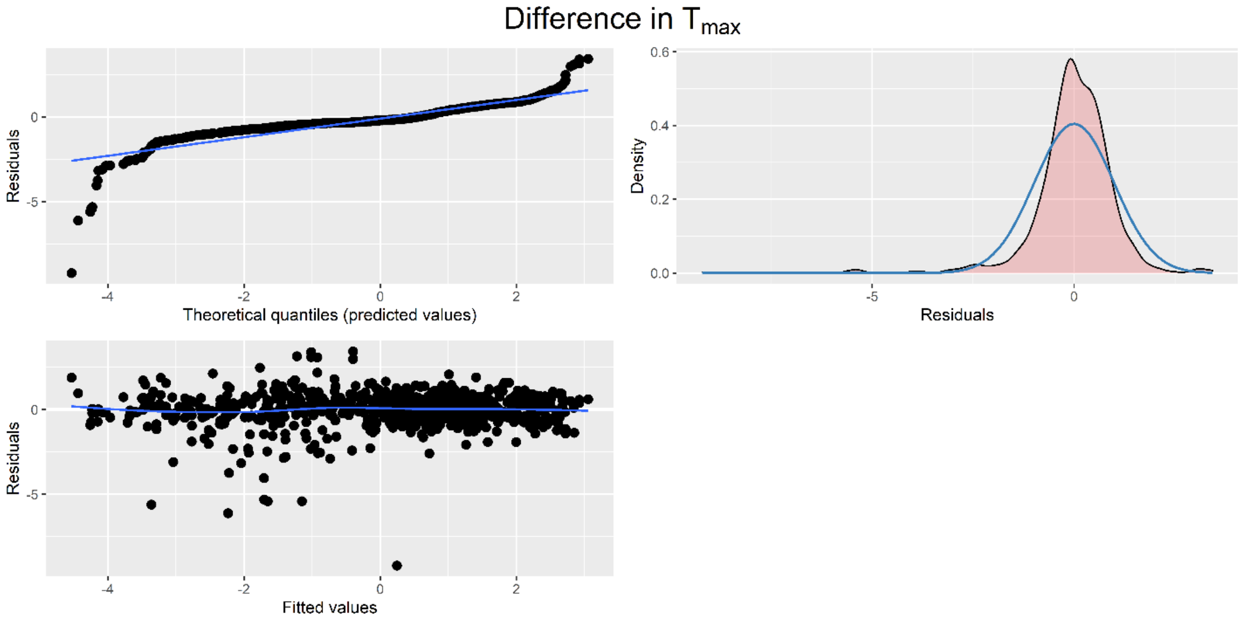


Figure S1.41: Model diagnostics for the absolute difference in monthly average of the daily maxima temperature between ClimateNA and iButton readings ($T_{Difference}$ = $T_{ClimateNA}$ - $T_{iButton}$) for the *winter* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *scaled* variables.

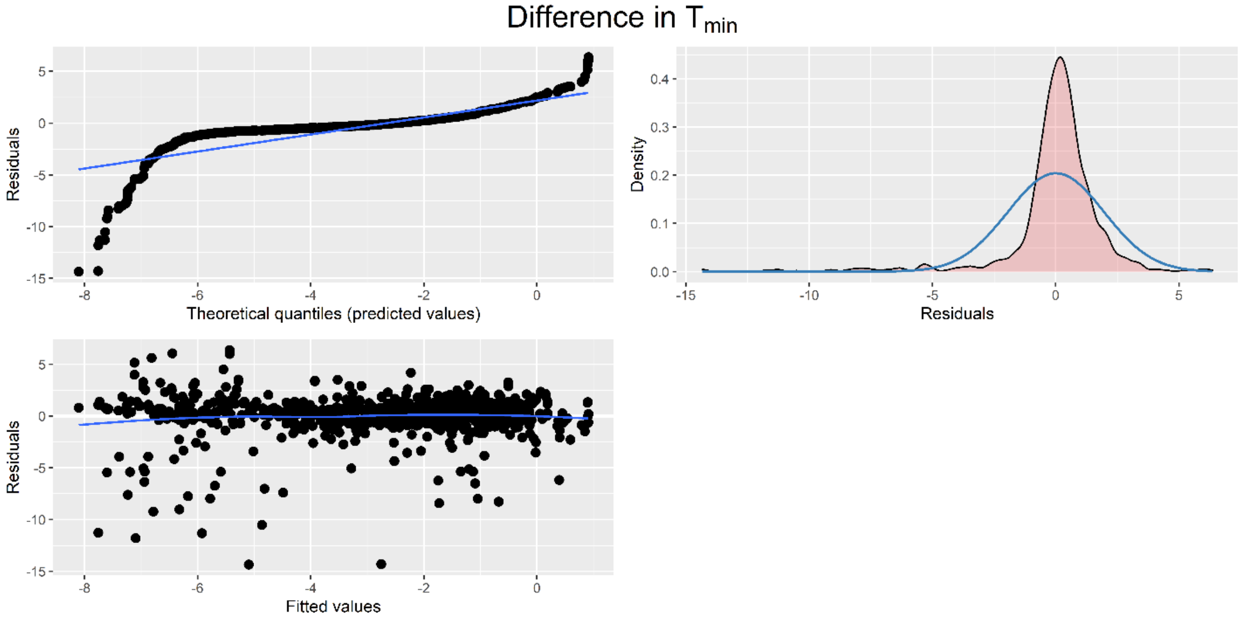


Figure S1.42: Model diagnostics for the absolute difference in monthly average of the daily minimum temperature between ClimateNA and iButton readings ($T_{Difference}$ = $T_{ClimateNA}$ - $T_{iButton}$) for the *winter* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *scaled* variables.

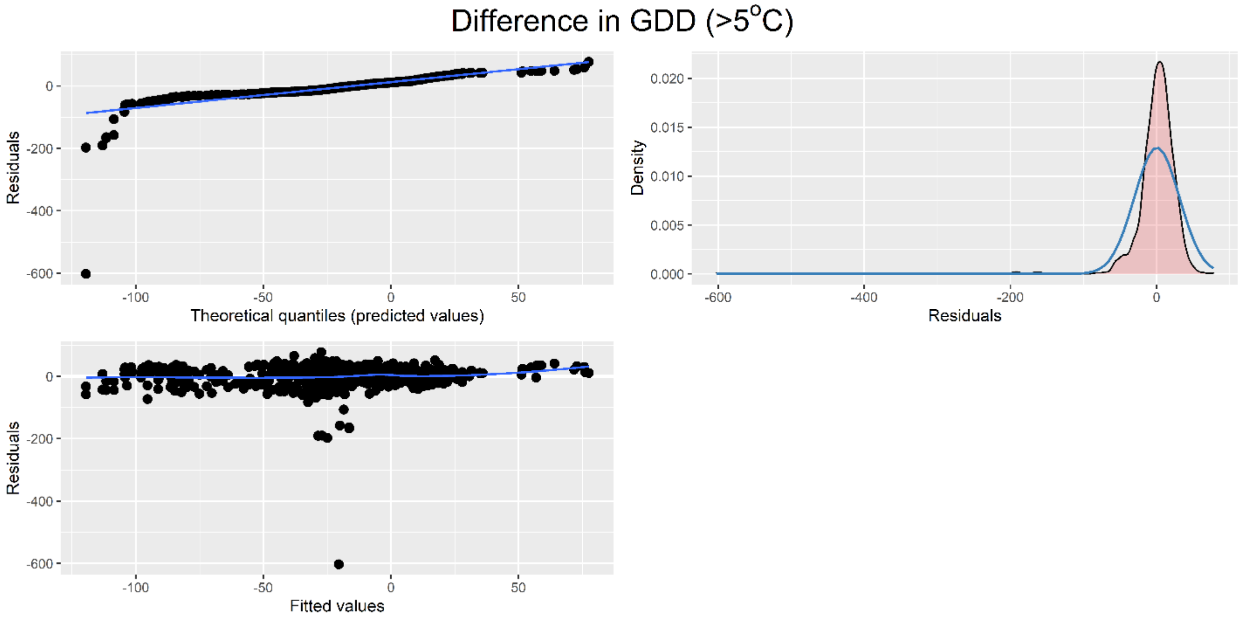


Figure S1.43: Model diagnostics for the absolute difference in monthly average growing degree days above 5 ˚C between ClimateNA and iButton readings ($T_{Difference} = T_{ClimateNA} - T_{iButton}$) for the *summer* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *unscaled* variables.

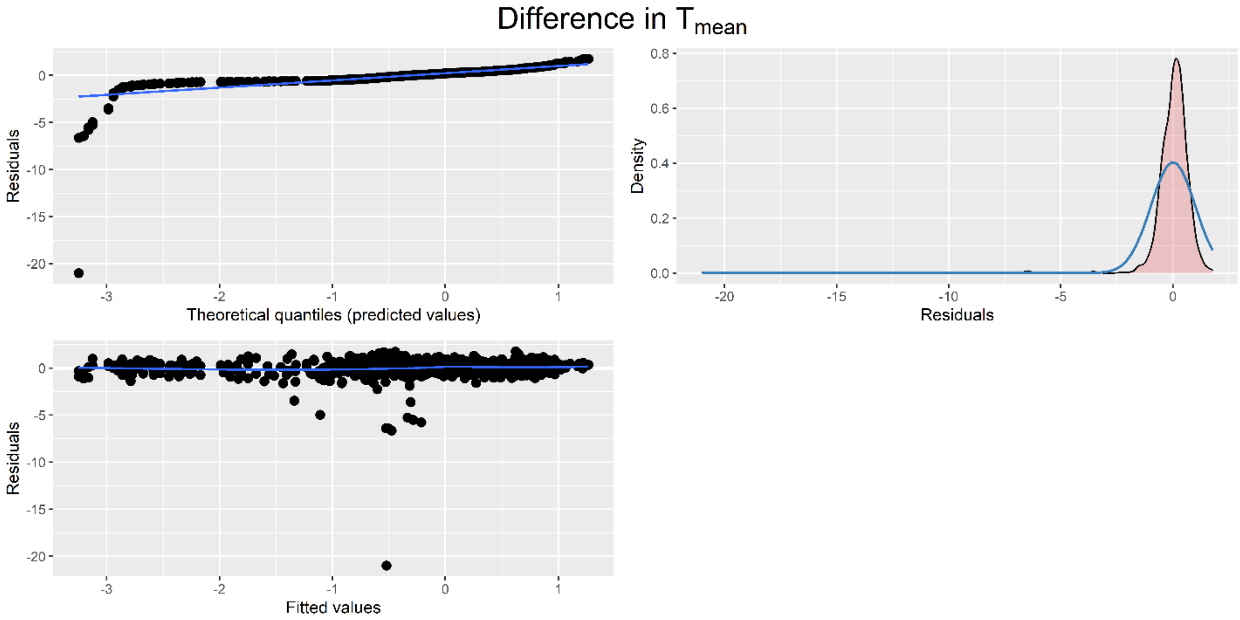


Figure S1.44: Model diagnostics for the absolute difference in monthly average of the daily mean temperature between ClimateNA and iButton readings ($T_{Difference} = T_{ClimateNA} - T_{iButton}$) for the *summer* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *unscaled* variables.

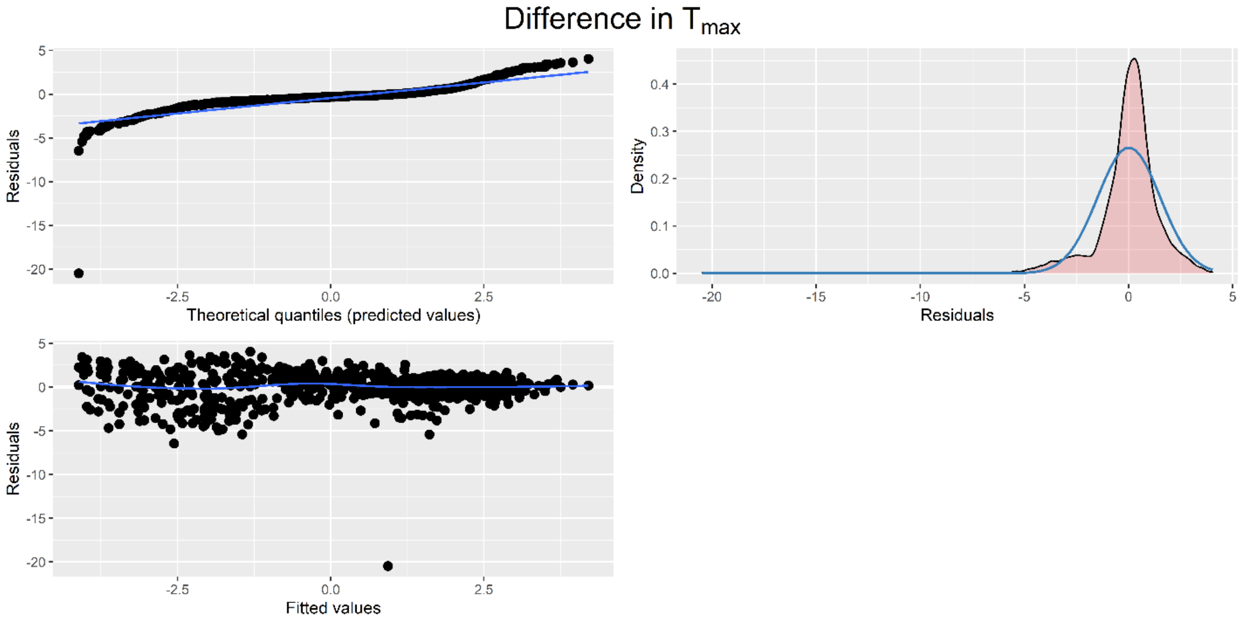


Figure S1.45: Model diagnostics for the absolute difference in monthly average of the daily maxima temperature between ClimateNA and iButton readings ($T_{Difference}$ = $T_{ClimateNA}$ - $T_{iButton}$) for the *summer* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *unscaled* variables.

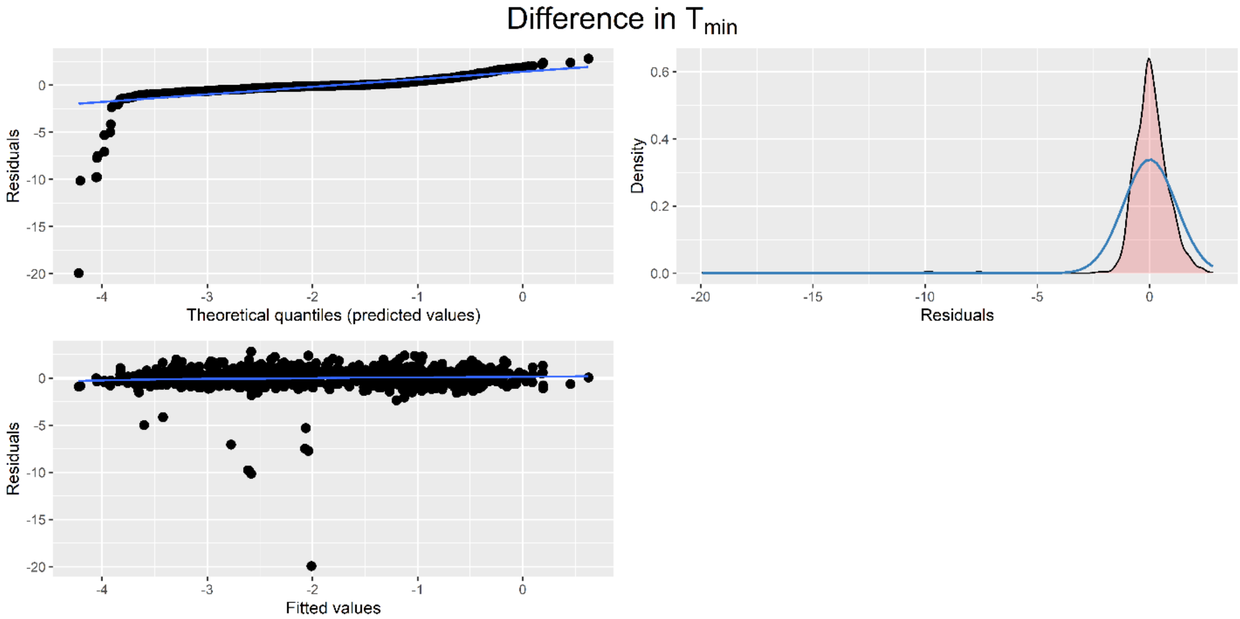


Figure S1.46: Model diagnostics for the absolute difference in monthly average of the daily minimum temperature between ClimateNA and iButton readings ($T_{Difference}$ = $T_{ClimateNA}$ - $T_{iButton}$) for the *summer* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *unscaled* variables.

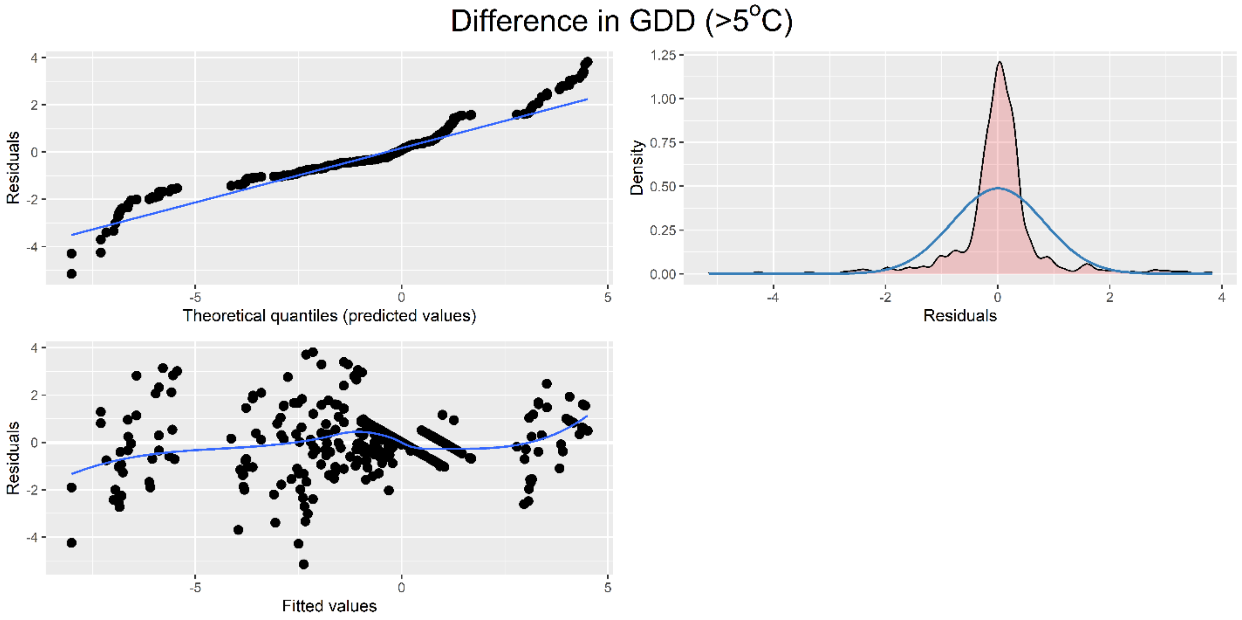


Figure S1.47: Model diagnostics for the absolute difference in monthly average growing degree days above 5 ˚C between ClimateNA and iButton readings ($T_{Difference} = T_{ClimateNA} - T_{iButton}$) for the *winter* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *unscaled* variables.

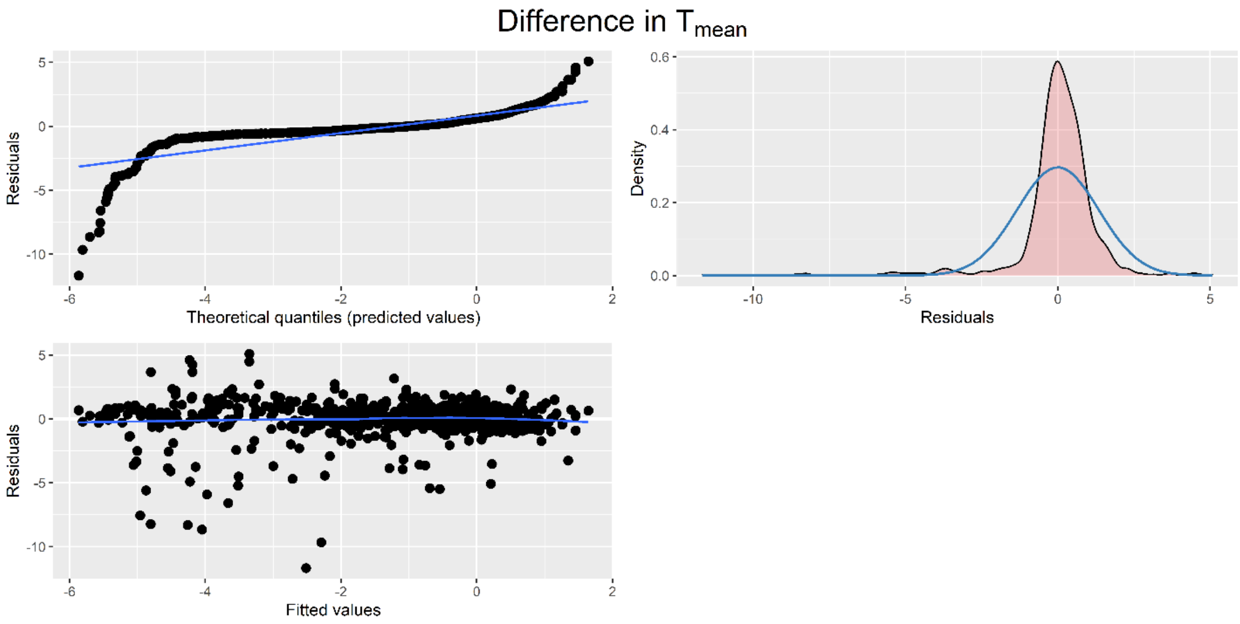


Figure S1.48: Model diagnostics for the absolute difference in monthly average of the daily mean temperature between ClimateNA and iButton readings ($T_{Difference} = T_{ClimateNA} - T_{iButton}$) for the *winter* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *unscaled* variables.

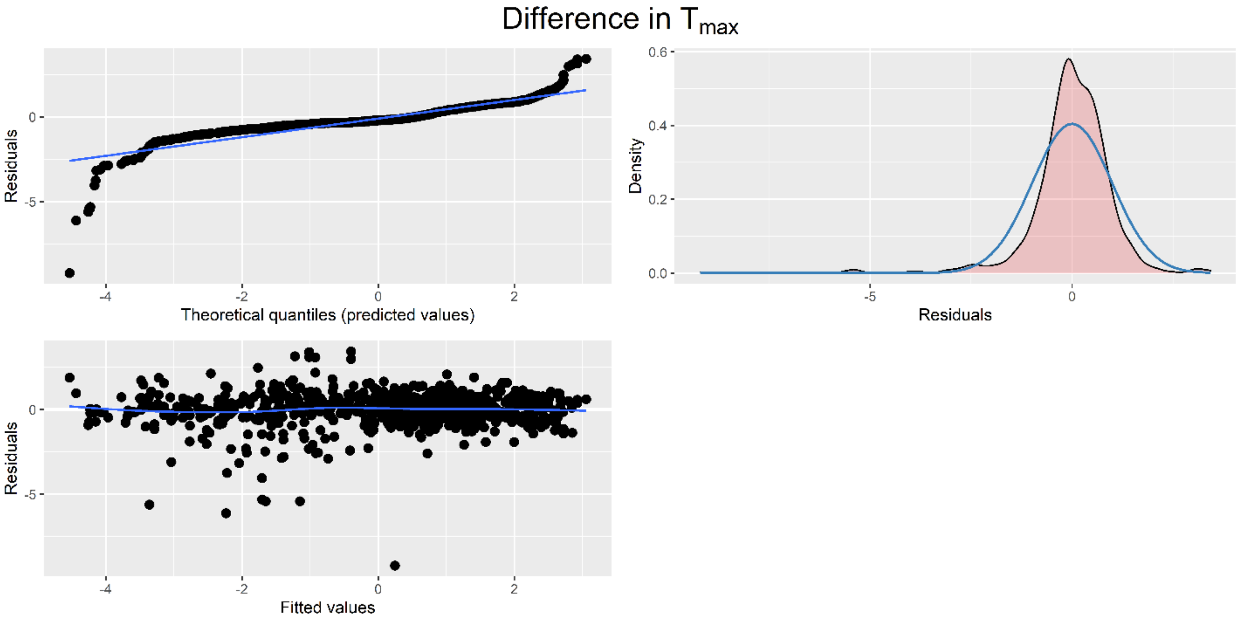
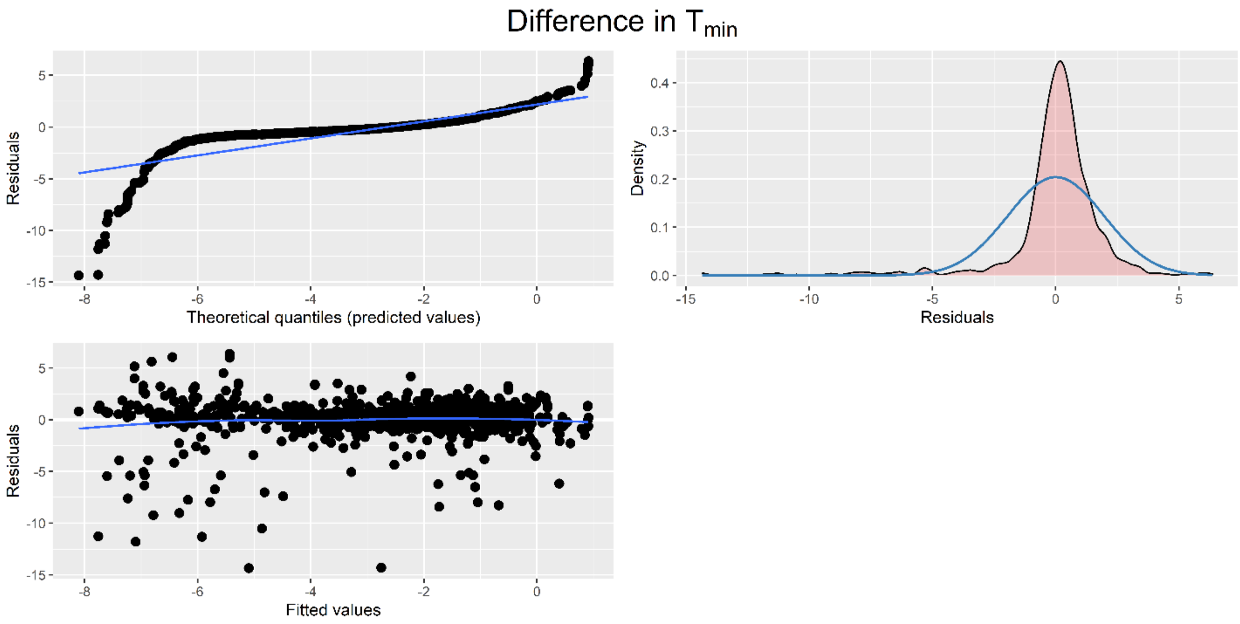


Figure S1.49: Model diagnostics for the absolute difference in monthly average of the daily maxima temperature between ClimateNA and iButton readings ($T_{Difference}$ = $T_{ClimateNA}$ - $T_{iButton}$) for the *winter* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *unscaled* variables.



Difference in T_{min}

Figure S1.50: Model diagnostics for the absolute difference in monthly average of the daily minimum temperature between ClimateNA and iButton readings ($T_{Difference}$ = $T_{ClimateNA}$ - $T_{iButton}$) for the *winter* season in hill and valley systems in Alberta, Canada. Residuals are for the *full model* with *unscaled* variables.

Appendix S2

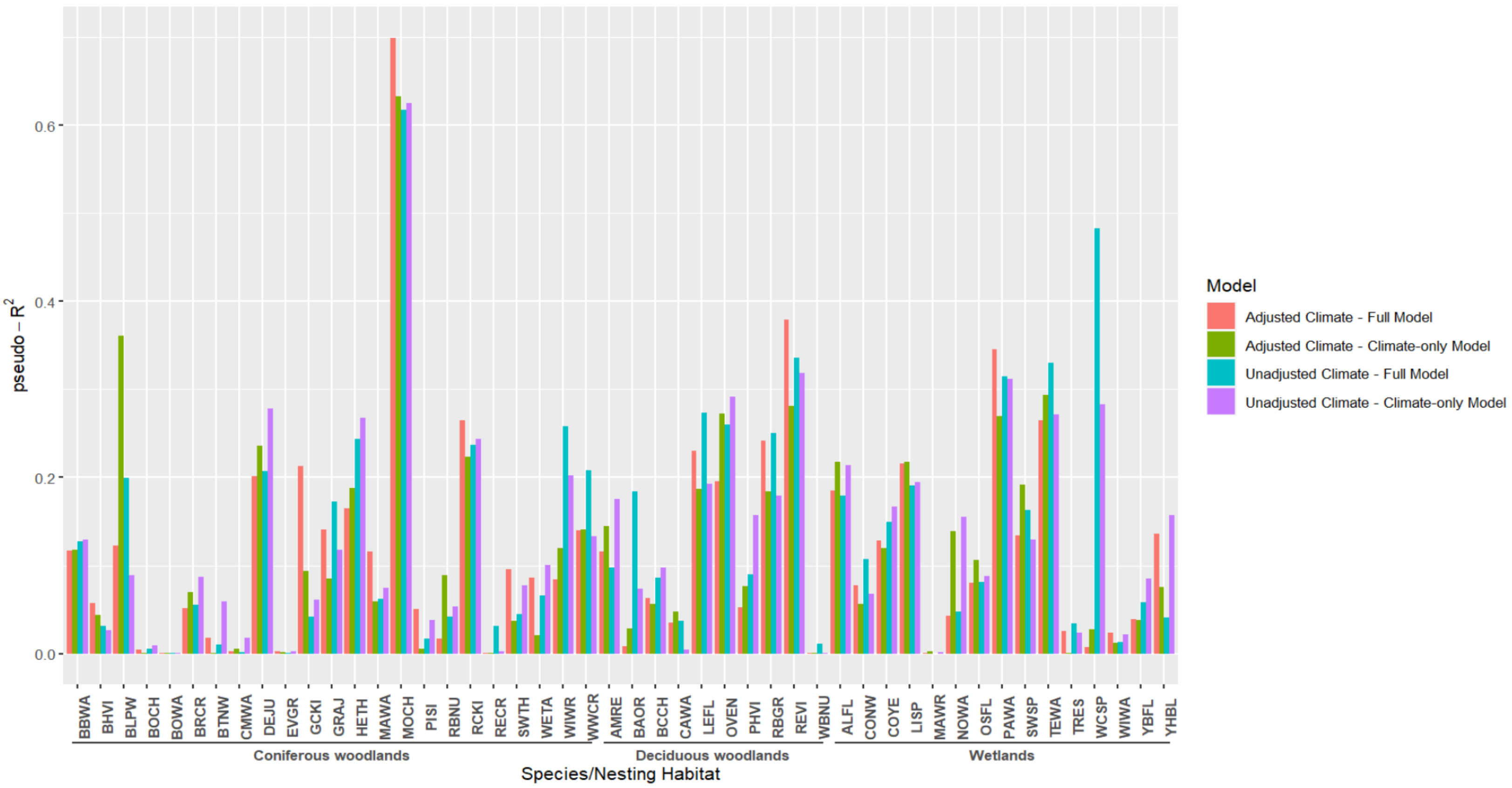


Figure S2.1: Individual species pseudo-R^2 values per model type. Labels beneath species names indicate their nesting habitat.

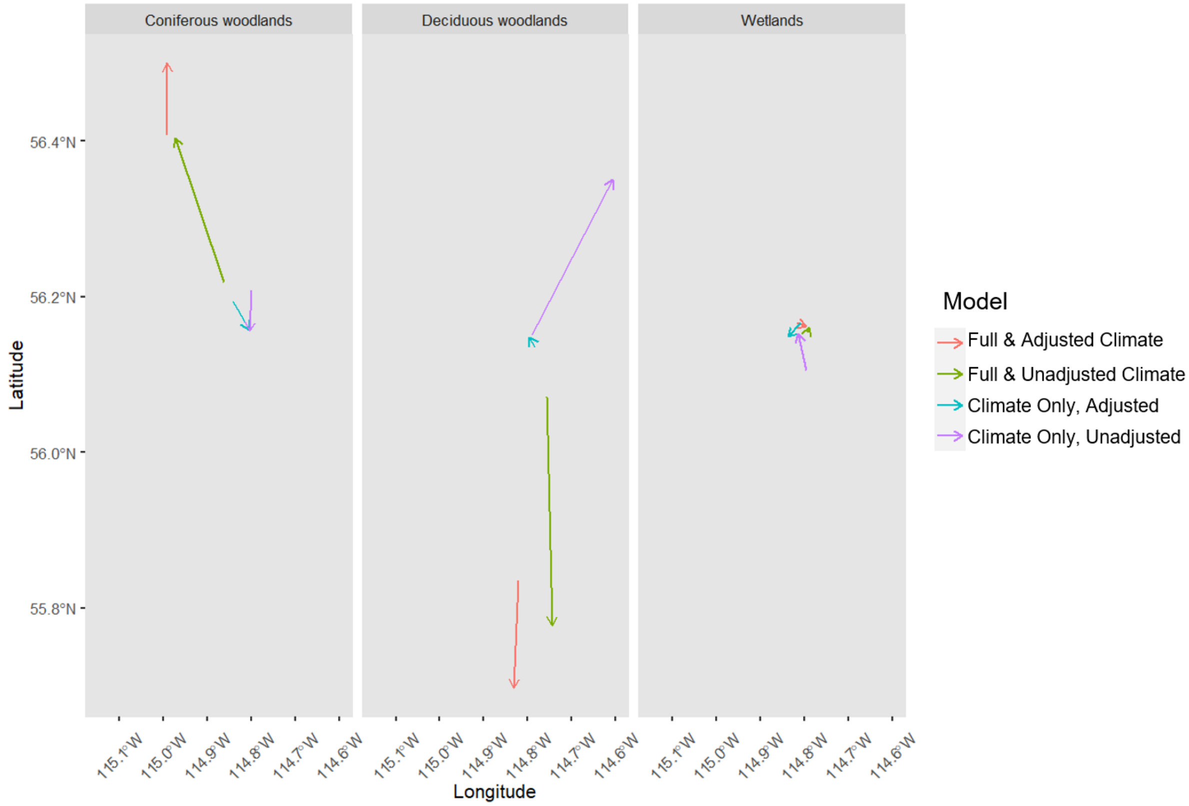


Figure S2.2: Change in refugia centroid, relative to current distribution, for different songbird groups in Alberta, Canada according to model type. Full models include vegetation and habitat effects on refugia, while adjusted indicates that some climate variables were downscaled to account for local topography and canopy cover effects. The beginning of each arrow indicates the position of the centroid for the current distribution, while the end of each arrow indicates the position of the refugia centroid by the end of the century (2080-2100) under a moderate climate scenario (SSP370)

Table S2.1: Relative influence of adjusted and unadjusted environmental variables on the occurrence of boreal songbirds in Alberta, Canada. Adjusted and unadjusted columns indicate the relative influence (weighted by the species pseudo-R^2) of a given variable with adjusted or unadjusted climate variables.

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated	BBWA	Bay-breasted Warbler	*Dendroica castanea*	Climate	CMI	1.069	1.314	6	5
					GDD>5	0.684	0.808	9	8
					Summer Precip	0.456	0.360	11	12
					Tmin	1.089	0.650	5	9
				Habitat	Crown Clsr	1.366	1.532	3	3
					NDVI	1.181	1.422	4	4
					Patch Area	0.756	0.934	8	6
					Tree Age	1.440	1.551	2	2
					Wet Probabilty	0.414	0.394	12	11
				Vegetation	B Spruce	0.908	0.841	7	7
					Birch	0.612	0.597	10	10
					Poplars	0.003	0.020	13	13
					W Spruce	1.667	2.302	1	1
	BHVI	Blue-headed Vireo	*Vireo solitarius*	Climate	CMI	0.802	0.614	1	1
					GDD>5	0.440	0.255	6	5
					Summer Precip	0.357	0.144	10	10
					Tmin	0.386	0.188	9	7
				Habitat	Crown Clsr	0.592	0.207	4	6
					NDVI	0.655	0.379	3	3
					Patch Area	0.414	0.185	8	9
					Tree Age	0.433	0.187	7	8
					Wet Probabilty	0.241	0.133	11	11
				Vegetation	B Spruce	0.502	0.306	5	4
					Birch	0.166	0.090	12	12
					Poplars	0.030	0.007	13	13
					W Spruce	0.663	0.405	2	2

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated (cont.)	BLPW	Blackpoll Warbler	*Dendroica striata*	Climate	CMI	1.403	1.103	4	8
					GDD>5	1.243	2.616	5	4
					Summer Precip	0.297	0.878	10	10
					Tmin	1.147	0.777	6	11
				Habitat	Crown Clsr	0.950	1.845	7	5
					NDVI	0.442	1.209	9	7
					Patch Area	0.484	1.228	8	6
					Tree Age	0.273	0.942	11	9
					Wet Probabilty	2.260	3.434	1	1
				Vegetation	B Spruce	1.843	2.957	3	2
					Birch	0.022	0.009	12	12
					Poplars	0.000	0.000	13	13
					W Spruce	1.883	2.945	2	3
	BOCH	Boreal Chickadee	*Poecile hudsonicus*	Climate	CMI	0.028	0.045	10	7
					GDD>5	0.045	0.048	6	2
					Summer Precip	0.021	0.021	11	11
					Tmin	0.035	0.038	7	10
				Habitat	Crown Clsr	0.033	0.039	8	9
					NDVI	0.045	0.042	5	8
					Patch Area	0.049	0.047	3	4
					Tree Age	0.049	0.047	2	3
					Wet Probabilty	0.031	0.046	9	6
				Vegetation	B Spruce	0.067	0.085	1	1
					Birch	0.008	0.010	12	12
					Poplars	0.000	0.000	13	13
					W Spruce	0.047	0.046	4	5

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated (cont.)	BOWA	Bohemian Waxwing	*Bombycilla garrulus*	Climate	CMI	0.001	0.000	2	9
					GDD>5	0.000	0.000	8	7
					Summer Precip	0.000	0.000	7	12
					Tmin	0.000	0.000	5	10
				Habitat	Crown Clsr	0.000	0.000	10	6
					NDVI	0.002	0.002	1	2
					Patch Area	0.000	0.000	4	4
					Tree Age	0.000	0.000	9	5
					Wet Probabilty	0.000	0.000	12	8
				Vegetation	B Spruce	0.000	0.000	3	11
					Birch	0.000	0.000	13	13
					Poplars	0.000	0.003	11	1
					W Spruce	0.000	0.001	6	3
	BRCR	Brown Creeper	*Certhia americana*	Climate	CMI	0.493	0.793	5	1
					GDD>5	0.421	0.594	7	5
					Summer Precip	0.296	0.300	10	10
					Tmin	0.300	0.326	9	9
				Habitat	Crown Clsr	0.642	0.725	1	2
					NDVI	0.485	0.464	6	7
					Patch Area	0.589	0.620	4	3
					Tree Age	0.633	0.616	2	4
					Wet Probabilty	0.132	0.062	12	12
				Vegetation	B Spruce	0.604	0.471	3	6
					Birch	0.179	0.187	11	11
					Poplars	0.003	0.004	13	13
					W Spruce	0.342	0.336	8	8

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated (cont.)	BTNW	Black-throated Green Warbler	*Dendroica virens*	Climate	CMI	0.224	0.129	3	3
					GDD>5	0.160	0.084	6	6
					Summer Precip	0.074	0.056	11	9
					Tmin	0.090	0.073	9	7
				Habitat	Crown Clsr	0.300	0.157	1	1
					NDVI	0.130	0.062	7	8
					Patch Area	0.192	0.100	4	5
					Tree Age	0.081	0.056	10	10
					Wet Probabilty	0.005	0.002	12	13
				Vegetation	B Spruce	0.102	0.040	8	11
					Birch	0.172	0.101	5	4
					Poplars	0.004	0.007	13	12
					W Spruce	0.251	0.144	2	2
	CMWA	Cape May Warbler	*Dendroica tigrina*	Climate	CMI	0.014	0.017	8	3
					GDD>5	0.027	0.020	2	2
					Summer Precip	0.012	0.007	11	11
					Tmin	0.018	0.013	5	6
				Habitat	Crown Clsr	0.017	0.012	7	7
					NDVI	0.012	0.009	10	10
					Patch Area	0.017	0.012	6	8
					Tree Age	0.026	0.014	3	4
					Wet Probabilty	0.012	0.011	9	9
				Vegetation	B Spruce	0.031	0.021	1	1
					Birch	0.007	0.004	12	12
					Poplars	0.003	0.001	13	13
					W Spruce	0.024	0.014	4	5

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated (cont.)	DEJU	Dark-eyed Junco	*Junco hyemalis*	Climate	CMI	1.373	0.955	7	9
					GDD>5	1.884	2.579	4	3
					Summer Precip	0.862	0.718	10	11
					Tmin	1.569	1.551	6	6
				Habitat	Crown Clsr	1.709	1.742	5	5
					NDVI	3.453	3.345	1	2
					Patch Area	0.988	1.213	9	8
					Tree Age	1.193	1.288	8	7
					Wet Probabilty	3.248	4.025	2	1
				Vegetation	B Spruce	2.712	2.155	3	4
					Birch	0.439	0.427	12	12
					Poplars	0.000	0.001	13	13
					W Spruce	0.723	0.726	11	10
	EVGR	Evening Grosbeak	*Coccothraustes vespertinus*	Climate	CMI	0.023	0.001	4	6
					GDD>5	0.026	0.001	2	4
					Summer Precip	0.011	0.000	10	10
					Tmin	0.021	0.001	6	8
				Habitat	Crown Clsr	0.025	0.002	3	2
					NDVI	0.020	0.001	7	7
					Patch Area	0.022	0.001	5	3
					Tree Age	0.040	0.002	1	1
					Wet Probabilty	0.004	0.000	12	12
				Vegetation	B Spruce	0.019	0.001	8	5
					Birch	0.007	0.000	11	11
					Poplars	0.000	0.000	13	13
					W Spruce	0.018	0.001	9	9

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated (cont.)	GCKI	Golden-crowned Kinglet	*Regulus satrapa*	Climate	CMI	3.948	1.198	1	1
					GDD>5	0.717	0.163	10	9
					Summer Precip	2.003	0.213	4	7
					Tmin	1.223	0.268	9	5
				Habitat	Crown Clsr	1.572	0.372	6	4
					NDVI	1.385	0.212	7	8
					Patch Area	1.287	0.233	8	6
					Tree Age	3.641	0.664	2	3
					Wet Probabilty	0.319	0.025	12	12
				Vegetation	B Spruce	1.588	0.120	5	10
					Birch	0.354	0.048	11	11
					Poplars	0.000	0.000	13	13
					W Spruce	3.306	0.690	3	2
	GRAJ	Gray Jay	*Perisoreus canadensis*	Climate	CMI	1.038	1.614	8	4
					GDD>5	1.555	1.730	3	3
					Summer Precip	0.739	0.689	10	10
					Tmin	1.375	1.577	4	5
				Habitat	Crown Clsr	1.103	1.436	6	7
					NDVI	1.068	1.570	7	6
					Patch Area	0.870	0.986	9	9
					Tree Age	1.261	1.408	5	8
					Wet Probabilty	1.807	2.126	2	2
				Vegetation	B Spruce	2.269	2.944	1	1
					Birch	0.413	0.455	12	12
					Poplars	0.015	0.038	13	13
					W Spruce	0.570	0.665	11	11

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated (cont.)	HETH	Hermit Thrush	*Catharus guttatus*	Climate	CMI	1.740	2.380	3	5
					GDD>5	2.538	3.584	1	1
					Summer Precip	0.985	0.871	10	12
					Tmin	1.152	2.399	7	4
				Habitat	Crown Clsr	1.673	2.697	4	3
					NDVI	1.435	2.022	5	6
					Patch Area	0.576	1.111	12	10
					Tree Age	1.342	1.392	6	9
					Wet Probabilty	0.986	1.489	9	8
				Vegetation	B Spruce	2.366	3.580	2	2
					Birch	0.681	1.033	11	11
					Poplars	0.031	0.105	13	13
					W Spruce	1.017	1.751	8	7
	MAWA	Magnolia Warbler	*Dendroica magnolia*	Climate	CMI	1.083	0.637	4	3
					GDD>5	1.141	0.505	3	8
					Summer Precip	0.596	0.241	12	12
					Tmin	1.067	0.662	6	2
				Habitat	Crown Clsr	1.075	0.519	5	7
					NDVI	1.256	0.730	1	1
					Patch Area	0.745	0.432	9	9
					Tree Age	1.162	0.560	2	5
					Wet Probabilty	1.041	0.595	7	4
				Vegetation	B Spruce	1.036	0.552	8	6
					Birch	0.599	0.393	11	11
					Poplars	0.026	0.014	13	13
					W Spruce	0.734	0.407	10	10

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated (cont.)	MOCH	Mountain Chickadee	*Poecile gambeli*	Climate	CMI	3.751	0.628	3	7
					GDD>5	55.809	49.192	1	1
					Summer Precip	2.026	1.412	5	4
					Tmin	3.837	3.786	2	3
				Habitat	Crown Clsr	2.908	5.187	4	2
					NDVI	0.646	0.640	7	6
					Patch Area	0.226	0.149	8	8
					Tree Age	0.778	0.767	6	5
					Wet Probabilty	0.009	0.014	9	9
				Vegetation	B Spruce	0.000	0.000	10	13
					Birch	0.000	0.000	11	10
					Poplars	0.000	0.000	12	12
					W Spruce	0.000	0.000	13	11
	PISI	Pine Siskin	*Carduelis pinus*	Climate	CMI	0.405	0.178	7	3
					GDD>5	0.590	0.178	2	4
					Summer Precip	0.380	0.124	9	8
					Tmin	0.496	0.119	4	9
				Habitat	Crown Clsr	0.392	0.139	8	6
					NDVI	0.364	0.162	10	5
					Patch Area	0.430	0.109	5	10
					Tree Age	0.635	0.220	1	2
					Wet Probabilty	0.313	0.131	11	7
				Vegetation	B Spruce	0.547	0.229	3	1
					Birch	0.113	0.030	12	12
					Poplars	0.003	0.000	13	13
					W Spruce	0.408	0.103	6	11

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated (cont.)	RBNU	Red-breasted Nuthatch	*Sitta canadensis*	Climate	CMI	0.169	0.530	4	2
					GDD>5	0.103	0.242	10	8
					Summer Precip	0.121	0.168	8	10
					Tmin	0.133	0.457	6	4
				Habitat	Crown Clsr	0.200	0.491	2	3
					NDVI	0.133	0.330	7	7
					Patch Area	0.141	0.405	5	6
					Tree Age	0.266	0.663	1	1
					Wet Probabilty	0.043	0.098	12	12
				Vegetation	B Spruce	0.104	0.182	9	9
					Birch	0.050	0.162	11	11
					Poplars	0.001	0.006	13	13
					W Spruce	0.199	0.448	3	5
	RCKI	Ruby-crowned Kinglet	*Regulus calendula*	Climate	CMI	2.472	1.481	4	5
					GDD>5	3.078	2.832	3	3
					Summer Precip	0.712	1.048	11	10
					Tmin	1.743	1.331	6	7
				Habitat	Crown Clsr	1.347	1.404	8	6
					NDVI	2.034	1.658	5	4
					Patch Area	1.166	1.157	9	8
					Tree Age	1.537	1.155	7	9
					Wet Probabilty	3.373	3.279	2	2
				Vegetation	B Spruce	7.333	6.830	1	1
					Birch	0.594	0.529	12	12
					Poplars	0.280	0.210	13	13
					W Spruce	0.815	0.743	10	11

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated (cont.)	RECR	Red Crossbill	*Loxia curvirostra*	Climate	CMI	0.003	0.130	3	10
					GDD>5	0.003	0.725	2	1
					Summer Precip	0.004	0.081	1	12
					Tmin	0.002	0.614	7	2
				Habitat	Crown Clsr	0.001	0.158	10	8
					NDVI	0.002	0.433	6	3
					Patch Area	0.001	0.146	9	9
					Tree Age	0.003	0.163	4	7
					Wet Probabilty	0.001	0.126	11	11
				Vegetation	B Spruce	0.003	0.170	5	6
					Birch	0.001	0.188	12	4
					Poplars	0.000	0.000	13	13
					W Spruce	0.001	0.171	8	5
	SWTH	Swainson's Thrush	*Catharus ustulatus*	Climate	CMI	0.661	0.303	9	9
					GDD>5	0.809	0.310	6	7
					Summer Precip	0.519	0.233	10	10
					Tmin	0.898	0.364	5	5
				Habitat	Crown Clsr	1.092	0.562	2	2
					NDVI	1.069	0.500	3	3
					Patch Area	0.752	0.359	7	6
					Tree Age	1.213	0.660	1	1
					Wet Probabilty	0.426	0.198	11	11
				Vegetation	B Spruce	0.945	0.426	4	4
					Birch	0.418	0.187	12	12
					Poplars	0.051	0.031	13	13
					W Spruce	0.680	0.303	8	8

Nesting Habitat	**Species Code**	**English Name**	**Scientific Name**	**Variable Type**	**Variable**	**Relative Influence**		**Importance Ranking**	
						Adj. Clim.	**Unadj. Clim.**	**Adj. Clim.**	**Unadj. Clim.**
Coniferous-associated (cont.)	WETA	Western Tanager	*Piranga ludoviciana*	Climate	CMI	0.750	0.703	5	3
					GDD>5	0.660	0.523	8	7
					Summer Precip	0.440	0.255	10	11
					Tmin	0.598	0.501	9	8
				Habitat	Crown Clsr	0.725	0.529	6	6
					NDVI	0.756	0.477	4	9
					Patch Area	0.698	0.560	7	5
					Tree Age	1.229	1.021	1	1
					Wet Probabilty	0.316	0.239	12	12
				Vegetation	B Spruce	0.883	0.743	3	2
					Birch	0.333	0.388	11	10
					Poplars	0.102	0.051	13	13
					W Spruce	1.087	0.633	2	4
	WIWR	Winter Wren	*Troglodytes troglodytes*	Climate	CMI	1.364	4.578	1	1
					GDD>5	0.727	1.847	6	9
					Summer Precip	0.972	1.984	2	6
					Tmin	0.756	2.287	5	4
				Habitat	Crown Clsr	0.523	1.688	10	11
					NDVI	0.621	1.939	8	7
					Patch Area	0.653	2.241	7	5
					Tree Age	0.813	2.636	4	2
					Wet Probabilty	0.101	0.518	12	12
				Vegetation	B Spruce	0.896	2.477	3	3
					Birch	0.469	1.696	11	10
					Poplars	0.011	0.106	13	13
					W Spruce	0.554	1.849	9	8

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Coniferous-associated (cont.)	WWCR	White-winged Crossbill	*Loxia leucoptera*	Climate	CMI	0.898	2.616	9	3
					GDD>5	1.559	1.913	3	4
					Summer Precip	1.730	0.991	2	10
					Tmin	1.019	2.668	6	2
				Habitat	Crown Clsr	1.196	1.858	5	5
					NDVI	0.987	1.588	7	7
					Patch Area	1.288	1.820	4	6
					Tree Age	0.822	1.582	10	8
					Wet Probabilty	0.501	0.842	11	11
				Vegetation	B Spruce	2.906	3.631	1	1
					Birch	0.138	0.191	12	12
					Poplars	0.000	0.000	13	13
					W Spruce	0.963	1.077	8	9

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Deciduous-associated	AMRE	American Redstart	*Setophaga ruticilla*	Climate	CMI	0.589	0.739	9	5
					GDD>5	1.318	1.247	2	2
					Summer Precip	0.748	0.684	8	7
					Tmin	0.976	0.738	5	6
				Habitat	Crown Clsr	0.906	0.782	6	4
					NDVI	2.406	2.002	1	1
					Patch Area	0.798	0.650	7	9
					Tree Age	1.112	0.938	3	3
					Wet Probabilty	0.558	0.506	11	10
				Vegetation	B Spruce	0.460	0.403	12	12
					Birch	0.567	0.451	10	11
					Poplars	0.001	0.000	13	13
					W Spruce	1.106	0.658	4	8
	BAOR	Baltimore Oriole	*Icterus galbula*	Climate	CMI	0.151	2.663	2	3
					GDD>5	0.268	2.525	1	4
					Summer Precip	0.099	3.452	3	1
					Tmin	0.069	3.371	5	2
				Habitat	Crown Clsr	0.066	1.777	6	6
					NDVI	0.071	1.983	4	5
					Patch Area	0.039	1.015	8	8
					Tree Age	0.051	1.125	7	7
					Wet Probabilty	0.012	0.184	10	10
				Vegetation	B Spruce	0.001	0.011	11	12
					Birch	0.001	0.030	12	11
					Poplars	0.000	0.000	13	13
					W Spruce	0.021	0.294	9	9

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Deciduous-associated (cont.)	BCCH	Black-capped Chickadee	*Poecile atricapillus*	Climate	CMI	0.603	0.976	5	3
					GDD>5	0.885	1.321	1	1
					Summer Precip	0.606	0.497	4	9
					Tmin	0.818	0.945	2	4
				Habitat	Crown Clsr	0.481	0.756	7	5
					NDVI	0.798	1.113	3	2
					Patch Area	0.374	0.479	9	10
					Tree Age	0.568	0.703	6	6
					Wet Probabilty	0.126	0.147	12	12
				Vegetation	B Spruce	0.299	0.528	10	8
					Birch	0.192	0.419	11	11
					Poplars	0.033	0.060	13	13
					W Spruce	0.478	0.633	8	7
	CAWA	Canada Warbler	*Wilsonia canadensis*	Climate	CMI	0.328	0.328	3	4
					GDD>5	0.249	0.269	6	7
					Summer Precip	0.104	0.120	11	11
					Tmin	0.144	0.269	9	6
				Habitat	Crown Clsr	0.533	0.504	2	2
					NDVI	0.873	0.814	1	1
					Patch Area	0.168	0.196	8	10
					Tree Age	0.247	0.198	7	9
					Wet Probabilty	0.076	0.077	12	12
				Vegetation	B Spruce	0.131	0.223	10	8
					Birch	0.296	0.305	5	5
					Poplars	0.005	0.032	13	13
					W Spruce	0.324	0.372	4	3

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Deciduous-associated (cont.)	LEFL	Least Flycatcher	*Empidonax minimus*	Climate	CMI	3.002	3.778	3	1
					GDD>5	3.056	3.216	2	4
					Summer Precip	2.153	1.730	5	8
					Tmin	2.531	3.541	4	3
				Habitat	Crown Clsr	1.541	2.220	8	7
					NDVI	3.162	3.616	1	2
					Patch Area	1.954	2.536	6	5
					Tree Age	1.390	1.679	10	9
					Wet Probabilty	0.403	0.650	11	11
				Vegetation	B Spruce	1.669	2.388	7	6
					Birch	0.340	0.401	13	12
					Poplars	0.401	0.342	12	13
					W Spruce	1.412	1.281	9	10
	OVEN	Ovenbird	*Seiurus aurocapillus*	Climate	CMI	1.628	2.420	5	5
					GDD>5	1.006	1.304	10	11
					Summer Precip	1.834	1.535	4	9
					Tmin	1.002	2.614	11	4
				Habitat	Crown Clsr	2.538	2.740	2	3
					NDVI	4.078	4.887	1	1
					Patch Area	1.347	1.454	6	10
					Tree Age	1.085	1.615	9	8
					Wet Probabilty	1.228	1.646	8	7
				Vegetation	B Spruce	1.996	2.961	3	2
					Birch	0.408	0.592	12	12
					Poplars	0.138	0.185	13	13
					W Spruce	1.306	2.031	7	6

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Deciduous-associated (cont.)	PHVI	Philadelphia Vireo	*Vireo philadelphicus*	Climate	CMI	0.218	0.794	10	4
					GDD>5	0.469	1.025	4	2
					Summer Precip	0.253	0.527	9	8
					Tmin	0.415	0.513	6	9
				Habitat	Crown Clsr	0.473	0.800	3	3
					NDVI	1.338	2.231	1	1
					Patch Area	0.339	0.535	8	7
					Tree Age	0.491	0.642	2	6
					Wet Probabilty	0.188	0.297	12	12
				Vegetation	B Spruce	0.468	0.722	5	5
					Birch	0.200	0.417	11	11
					Poplars	0.004	0.005	13	13
					W Spruce	0.346	0.512	7	10
	RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	Climate	CMI	2.608	2.097	2	5
					GDD>5	1.955	2.502	5	2
					Summer Precip	1.063	0.937	11	12
					Tmin	1.763	1.510	9	10
				Habitat	Crown Clsr	2.286	2.058	3	7
					NDVI	4.452	4.863	1	1
					Patch Area	1.886	1.845	7	8
					Tree Age	2.038	2.265	4	3
					Wet Probabilty	1.267	1.603	10	9
				Vegetation	B Spruce	1.836	2.068	8	6
					Birch	0.946	1.025	12	11
					Poplars	0.128	0.192	13	13
					W Spruce	1.955	2.114	6	4

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Deciduous-associated (cont.)	REVI	Red-eyed Vireo	*Vireo olivaceus*	Climate	CMI	2.200	2.788	10	5
					GDD>5	3.587	3.157	3	4
					Summer Precip	2.492	1.252	9	10
					Tmin	2.494	3.611	8	3
				Habitat	Crown Clsr	2.837	2.229	5	7
					NDVI	9.116	7.933	1	1
					Patch Area	2.903	2.060	4	8
					Tree Age	2.691	2.632	7	6
					Wet Probabilty	0.819	1.005	12	12
				Vegetation	B Spruce	4.555	4.052	2	2
					Birch	1.311	1.249	11	11
					Poplars	0.102	0.062	13	13
					W Spruce	2.781	1.549	6	9
	WBNU	White-breasted Nuthatch	*Sitta carolinensis*	Climate	CMI	0.000	0.104	5	3
					GDD>5	0.000	0.049	6	8
					Summer Precip	0.000	0.054	7	7
					Tmin	0.000	0.031	11	10
				Habitat	Crown Clsr	0.001	0.154	2	2
					NDVI	0.002	0.086	1	5
					Patch Area	0.000	0.055	9	6
					Tree Age	0.000	0.095	8	4
					Wet Probabilty	0.000	0.000	13	13
				Vegetation	B Spruce	0.000	0.012	12	12
					Birch	0.000	0.029	4	11
					Poplars	0.000	0.387	3	1
					W Spruce	0.000	0.048	10	9

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Wetland-associated	ALFL	Alder Flycatcher	*Empidonax alnorum*	Climate	CMI	1.552	1.764	7	3
					GDD>5	1.828	1.437	3	7
					Summer Precip	1.563	0.614	6	11
					Tmin	1.512	2.932	8	1
				Habitat	Crown Clsr	2.171	2.227	1	2
					NDVI	1.857	1.632	2	4
					Patch Area	1.801	1.514	4	5
					Tree Age	1.455	1.452	9	6
					Wet Probabilty	1.175	1.253	10	9
				Vegetation	B Spruce	1.779	1.348	5	8
					Birch	0.605	0.574	12	12
					Poplars	0.262	0.441	13	13
					W Spruce	0.990	0.699	11	10
	CONW	Connecticut Warbler	*Oporornis agilis*	Climate	CMI	0.683	0.866	6	6
					GDD>5	1.070	1.322	1	2
					Summer Precip	0.794	0.933	3	5
					Tmin	0.792	0.834	4	7
				Habitat	Crown Clsr	0.727	1.017	5	4
					NDVI	0.968	1.439	2	1
					Patch Area	0.577	0.806	8	8
					Tree Age	0.571	0.765	9	9
					Wet Probabilty	0.124	0.179	12	12
				Vegetation	B Spruce	0.640	1.253	7	3
					Birch	0.378	0.565	10	11
					Poplars	0.077	0.075	13	13
					W Spruce	0.376	0.645	11	10

Nesting Habitat	**Species Code**	**English Name**	**Scientific Name**	**Variable Type**	**Variable**	**Relative Influence**		**Importance Ranking**	
						Adj. Clim.	**Unadj. Clim.**	**Adj. Clim.**	**Unadj. Clim.**
Wetland-associated (cont.)	COYE	Common Yellowthroat	*Geothlypis trichas*	Climate	CMI	1.067	1.726	6	3
					GDD>5	1.572	2.041	2	1
					Summer Precip	0.921	0.659	9	10
					Tmin	1.133	1.449	5	5
				Habitat	Crown Clsr	1.957	1.972	1	2
					NDVI	0.996	1.291	7	7
					Patch Area	1.172	1.355	4	6
					Tree Age	1.357	1.450	3	4
					Wet Probabilty	0.765	0.883	10	9
				Vegetation	B Spruce	0.966	1.032	8	8
					Birch	0.418	0.341	11	12
					Poplars	0.136	0.141	13	13
					W Spruce	0.337	0.576	12	11
	LISP	Lincoln's Sparrow	*Melospiza lincolnii*	Climate	CMI	2.290	2.310	3	2
					GDD>5	2.510	1.794	2	6
					Summer Precip	1.460	0.709	8	11
					Tmin	2.030	1.898	6	5
				Habitat	Crown Clsr	2.911	2.886	1	1
					NDVI	2.050	1.942	5	4
					Patch Area	1.444	1.289	9	8
					Tree Age	1.201	1.060	10	9
					Wet Probabilty	2.204	2.178	4	3
				Vegetation	B Spruce	1.643	1.410	7	7
					Birch	0.466	0.322	13	13
					Poplars	0.498	0.371	12	12
					W Spruce	0.894	0.919	11	10

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Wetland-associated (cont.)	MAWR	Marsh Wren	*Cistothorus palustris*	Climate	CMI	0.001	0.000	7	5
					GDD>5	0.002	0.000	5	7
					Summer Precip	0.003	0.000	1	2
					Tmin	0.002	0.000	6	8
				Habitat	Crown Clsr	0.002	0.000	4	3
					NDVI	0.002	0.000	2	1
					Patch Area	0.001	0.000	9	9
					Tree Age	0.002	0.000	3	4
					Wet Probabilty	0.001	0.000	11	10
				Vegetation	B Spruce	0.001	0.000	8	6
					Birch	0.000	0.000	13	13
					Poplars	0.000	0.000	12	12
					W Spruce	0.001	0.000	10	11
	NOWA	Northern Waterthrush	*Seiurus noveboracensis*	Climate	CMI	0.295	0.403	7	6
					GDD>5	0.649	0.426	2	5
					Summer Precip	0.297	0.243	6	10
					Tmin	0.443	0.642	4	2
				Habitat	Crown Clsr	0.681	0.731	1	1
					NDVI	0.267	0.358	8	7
					Patch Area	0.184	0.316	10	8
					Tree Age	0.240	0.310	9	9
					Wet Probabilty	0.470	0.508	3	4
				Vegetation	B Spruce	0.438	0.532	5	3
					Birch	0.141	0.124	12	12
					Poplars	0.004	0.007	13	13
					W Spruce	0.167	0.142	11	11

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Wetland-associated (cont.)	OSFL	Olive-sided Flycatcher	*Contopus cooperi*	Climate	CMI	0.494	0.561	8	7
					GDD>5	1.196	1.495	1	1
					Summer Precip	0.323	0.337	9	10
					Tmin	0.723	0.377	6	9
				Habitat	Crown Clsr	0.978	1.005	4	3
					NDVI	1.071	1.273	2	2
					Patch Area	0.570	0.597	7	6
					Tree Age	0.320	0.422	10	8
					Wet Probabilty	0.789	0.719	5	5
				Vegetation	B Spruce	1.069	0.882	3	4
					Birch	0.140	0.137	12	12
					Poplars	0.116	0.060	13	13
					W Spruce	0.229	0.265	11	11
	PAWA	Palm Warbler	*Dendroica palmarum*	Climate	CMI	1.029	1.336	10	9
					GDD>5	2.864	2.854	5	4
					Summer Precip	1.365	1.237	9	10
					Tmin	2.816	2.032	6	6
				Habitat	Crown Clsr	3.498	2.711	3	5
					NDVI	3.404	2.881	4	3
					Patch Area	1.644	1.395	7	8
					Tree Age	1.496	1.685	8	7
					Wet Probabilty	11.653	11.106	1	1
				Vegetation	B Spruce	3.973	3.530	2	2
					Birch	0.118	0.093	12	12
					Poplars	0.025	0.000	13	13
					W Spruce	0.717	0.666	11	11

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Wetland-associated (cont.)	SWSP	Swamp Sparrow	*Melospiza georgiana*	Climate	CMI	0.858	1.497	8	6
					GDD>5	1.726	1.920	3	4
					Summer Precip	0.535	0.375	10	10
					Tmin	1.015	0.958	6	8
				Habitat	Crown Clsr	1.847	2.244	2	3
					NDVI	1.489	1.709	5	5
					Patch Area	0.970	1.279	7	7
					Tree Age	0.688	0.945	9	9
					Wet Probabilty	2.102	2.488	1	1
				Vegetation	B Spruce	1.599	2.274	4	2
					Birch	0.200	0.203	12	12
					Poplars	0.070	0.069	13	13
					W Spruce	0.357	0.319	11	11
	TEWA	Tennessee Warbler	*Vermivora peregrina*	Climate	CMI	2.844	3.568	4	3
					GDD>5	3.433	4.143	1	2
					Summer Precip	1.448	1.092	11	11
					Tmin	2.887	5.386	2	1
				Habitat	Crown Clsr	2.632	3.419	5	4
					NDVI	2.394	3.140	6	5
					Patch Area	2.064	2.142	7	8
					Tree Age	1.835	2.765	8	7
					Wet Probabilty	1.773	1.781	9	9
				Vegetation	B Spruce	2.858	2.869	3	6
					Birch	0.694	0.992	12	12
					Poplars	0.109	0.142	13	13
					W Spruce	1.494	1.590	10	10

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	**Unadj. Clim.**	**Adj. Clim.**	**Unadj. Clim.**
Wetland-associated (cont.)	TRES	Tree Swallow	*Tachycineta bicolor*	Climate	CMI	0.242	0.413	6	5
					GDD>5	0.420	0.469	1	3
					Summer Precip	0.313	0.328	4	6
					Tmin	0.312	0.523	5	1
				Habitat	Crown Clsr	0.357	0.416	2	4
					NDVI	0.335	0.481	3	2
					Patch Area	0.134	0.206	8	8
					Tree Age	0.200	0.219	7	7
					Wet Probabilty	0.009	0.010	12	12
				Vegetation	B Spruce	0.102	0.138	10	9
					Birch	0.023	0.028	11	11
					Poplars	0.000	0.000	13	13
					W Spruce	0.110	0.135	9	10
	WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*	Climate	CMI	0.124	8.600	1	3
					GDD>5	0.102	2.446	3	8
					Summer Precip	0.117	2.381	2	9
					Tmin	0.100	9.671	4	1
				Habitat	Crown Clsr	0.013	3.681	11	6
					NDVI	0.021	4.346	9	4
					Patch Area	0.027	8.850	8	2
					Tree Age	0.094	4.224	5	5
					Wet Probabilty	0.013	0.082	12	12
				Vegetation	B Spruce	0.035	0.175	6	11
					Birch	0.014	0.329	10	10
					Poplars	0.000	0.000	13	13
					W Spruce	0.027	3.489	7	7

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Wetland-associated (cont.)	WIWA	Wilson's Warbler	*Wilsonia pusilla*	Climate	CMI	0.168	0.050	7	10
					GDD>5	0.423	0.266	1	1
					Summer Precip	0.135	0.056	9	8
					Tmin	0.259	0.155	3	3
				Habitat	Crown Clsr	0.210	0.124	6	5
					NDVI	0.234	0.126	5	4
					Patch Area	0.155	0.080	8	7
					Tree Age	0.123	0.051	10	9
					Wet Probabilty	0.351	0.183	2	2
				Vegetation	B Spruce	0.238	0.112	4	6
					Birch	0.047	0.049	12	11
					Poplars	0.000	0.000	13	13
					W Spruce	0.060	0.048	11	12
	YBFL	Yellow-bellied Flycatcher	*Empidonax flaviventris*	Climate	CMI	0.363	0.477	4	6
					GDD>5	0.744	0.765	1	3
					Summer Precip	0.188	0.233	9	10
					Tmin	0.583	0.963	3	2
				Habitat	Crown Clsr	0.283	0.413	6	7
					NDVI	0.222	0.554	8	4
					Patch Area	0.167	0.253	10	9
					Tree Age	0.237	0.292	7	8
					Wet Probabilty	0.703	1.183	2	1
				Vegetation	B Spruce	0.324	0.529	5	5
					Birch	0.023	0.032	12	12
					Poplars	0.002	0.001	13	13
					W Spruce	0.100	0.161	11	11

Nesting Habitat	Species Code	English Name	Scientific Name	Variable Type	Variable	Relative Influence		Importance Ranking	
						Adj. Clim.	Unadj. Clim.	Adj. Clim.	Unadj. Clim.
Wetland-associated (cont.)	YHBL	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	Climate	CMI	4.101	0.522	1	3
					GDD>5	1.618	0.483	3	4
					Summer Precip	1.847	0.711	2	2
					Tmin	1.435	0.756	5	1
				Habitat	Crown Clsr	0.970	0.306	7	8
					NDVI	1.507	0.448	4	6
					Patch Area	0.962	0.449	8	5
					Tree Age	1.079	0.360	6	7
					Wet Probabilty	0.000	0.003	13	11
				Vegetation	B Spruce	0.020	0.006	10	10
					Birch	0.000	0.000	11	12
					Poplars	0.000	0.000	12	13
					W Spruce	0.058	0.037	9	9

Table S2.2: Mean and median end-of-century (2080-2100) refugia potential index for different songbird groups in Alberta, Canada under a moderate climate scenario (SSP370). Full models include vegetation and habitat effects on refugia, while adjusted indicates that some climate variables were downscaled to account for local topography and canopy cover effects. Models are sorted according to mean refugia.

Nesting Habitat	Model	Refugia Potential			
		Mean	Median	05th Percentile	95th Percentile
Coniferous-associated	Climate Only, Adjusted	0.36	0.31	0.08	0.69
	Climate Only, Unadjusted	0.37	0.30	0.10	0.70
	Full & Adjusted Climate	0.29	0.29	0.00	0.53
	Full & Unadjusted Climate	0.36	0.39	0.00	0.67
Deciduous-associated	Climate Only, Adjusted	0.37	0.29	0.14	0.71
	Climate Only, Unadjusted	0.36	0.38	0.00	0.88
	Full & Adjusted Climate	0.28	0.20	0.00	0.70
	Full & Unadjusted Climate	0.25	0.20	0.00	0.70
Wetland-associated	Climate Only, Adjusted	0.28	0.30	0.00	0.60
	Climate Only, Unadjusted	0.36	0.30	0.10	0.70
	Full & Adjusted Climate	0.33	0.21	0.07	0.79
	Full & Unadjusted Climate	0.37	0.29	0.07	0.86

Appendix S3

Table S3.1: Estimated direct, indirect, total and mediator effects of climate, forest structure and vegetation on coniferous-, deciduous-, and wetland-associated boreal songbirds in Alberta, Canada. Estimates are based on 10.000 bootstrap iterations based on piecewise structural equation models. Refer to Table 3.1 in the main text for variable descriptions and acronyms. SE – standard error; L CI/H CI – lower/higher 95% confidence intervals based; Sig. - significance

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Coniferous-associated	BBWA	Bay-breasted Warbler	*Dendroica castanea*	**Direct**	Climate	MSP	0	0.01	-0.01	0.01	
						CMI	0.022	0.01	0.013	0.032	*
						DD5	-0.035	0.01	-0.04	-0.03	*
					Forest Structure	NDVI	-0.018	0.01	-0.03	-0.01	*
						Psize	-0.026	0.01	-0.04	-0.01	*
						WetProb	-0.033	0.01	-0.04	-0.02	*
						Age	0.029	0.01	0.015	0.045	*
						Cclosure	-0.003	0.01	-0.02	0.01	
					Vegetation	Wspruce	0.017	0.01	0.001	0.035	*
						Bspruce	-0.001	0.01	-0.02	0.013	
						Birch	0.013	0.01	-0	0.035	
						Poplars	-0.01	0	-0.02	-0.01	*
				Indirect	Climate	MSP	-0.001	0.01	-0	0	
						CMI	0.002	0	-0	0.004	
						DD5	-0.001	0.01	-0	0.001	
						Tmin	-0.001	0	-0	0.001	
					Soil	tclay	0.001	0.1	0	0.002	
						tsand	0	0.09	0	0.001	
				Mediators	Vegetation	Wspruce	0.001	0	0	0.001	
						Bspruce	0	0.01	-0	0.002	
						Birch	0.001	0	0	0.002	
						Poplars	-0.001	0	-0	-0	*
				Total	Climate	MSP	-0.001	0.01	-0.01	0.009	
						CMI	0.024	0.01	0.015	0.033	*
						DD5	-0.036	0.01	-0.04	-0.03	*
						Tmin	-0.001	0	-0	0.001	
					Forest Structure	NDVI	-0.018	0.01	-0.03	-0.01	*
						Psize	-0.026	0.01	-0.04	-0.01	*
						WetProb	-0.033	0.01	-0.04	-0.02	*
						Age	0.029	0.01	0.015	0.045	*
						Cclosure	-0.003	0.01	-0.02	0.01	
					Soil	tclay	0.001	0.1	0	0.002	
						tsand	0	0.09	0	0.001	
					Vegetation	Wspruce	0.017	0.01	0.001	0.035	*
						Bspruce	-0.001	0.01	-0.02	0.013	
						Birch	0.013	0.01	-0	0.035	
						Poplars	-0.01	0	-0.02	-0.01	*

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Coniferous-associated (cont.)	BHVI	Blue-headed Vireo	*Vireo solitarius*	**Direct**	Climate	MSP	-0.018	0.01	-0.03	-0.01	*
						CMI	0.032	0.01	0.019	0.044	*
						DD5	-0.038	0.01	-0.05	-0.03	*
					Forest Structure	NDVI	-0.006	0.01	-0.02	0.005	
						Psize	0.007	0.01	-0.01	0.023	
						WetProb	-0.017	0.01	-0.03	0	
						Age	-0.009	0.01	-0.02	0.005	
						Cclosure	-0.001	0.01	-0.01	0.013	
					Vegetation	Wspruce	0.042	0.01	0.025	0.06	*
						Bspruce	0.014	0.01	-0	0.029	
						Birch	0.006	0.01	-0.01	0.028	
						Poplars	0.026	0.01	0.006	0.059	*
				Indirect	Climate	MSP	0.002	0.04	0	0.004	
						CMI	0.004	0.06	0.002	0.007	*
						DD5	-0.002	0.03	-0	0	
						Tmin	-0.003	0.05	-0	-0	*
					Soil	tclay	0.002	0.44	0	0.004	
						tsand	-0.001	0.36	-0	0	
				Mediators	Vegetation	Wspruce	0.002	0	0.001	0.003	*
						Bspruce	-0.002	0.07	-0	0	
						Birch	0	0	0	0.001	
						Poplars	0.002	0	0.001	0.006	*
				Total	Climate	MSP	-0.016	0.04	-0.03	-0	*
						CMI	0.036	0.06	0.024	0.047	*
						DD5	-0.04	0.03	-0.05	-0.03	*
						Tmin	-0.003	0.05	-0	-0	*
					Forest Structure	NDVI	-0.006	0.01	-0.02	0.005	
						Psize	0.007	0.01	-0.01	0.023	
						WetProb	-0.017	0.01	-0.03	0	
						Age	-0.009	0.01	-0.02	0.005	
						Cclosure	-0.001	0.01	-0.01	0.013	
					Soil	tclay	0.002	0.44	0	0.004	
						tsand	-0.001	0.36	-0	0	
					Vegetation	Wspruce	0.042	0.01	0.025	0.06	*
						Bspruce	0.014	0.01	-0	0.029	
						Birch	0.006	0.01	-0.01	0.028	
						Poplars	0.026	0.01	0.006	0.059	*

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Coniferous-associated (cont.)	BLPW	Blackpoll Warbler	*Dendroica striata*	**Direct**	Climate	MSP	-0.012	0.01	-0.03	0.002	
						CMI	0.003	0.01	-0.01	0.015	
						DD5	0.001	0.01	-0.01	0.013	
					Forest Structure	NDVI	0.017	0.01	0.007	0.027	*
						Psize	-0.048	0.01	-0.08	-0.02	*
						WetProb	-0.002	0.01	-0.02	0.026	
						Age	-0.015	0.01	-0.03	-0	*
						Cclosure	0.011	0.01	-0.01	0.035	
					Vegetation	Wspruce	0.048	0.02	0.021	0.083	*
						Bspruce	0.038	0.01	0.018	0.057	*
						Birch	-0.002	0.01	-0.01	0.011	
						Poplars	-0.009	0	-0.01	-0.01	*
				Indirect	Climate	MSP	-0.001	0.05	-0	0	
						CMI	0.007	0.09	0.004	0.011	*
						DD5	-0.005	0.05	-0.01	-0	*
						Tmin	-0.004	0.09	-0.01	-0	*
					Soil	tclay	-0.001	0.51	-0	0	
						tsand	0	0.42	-0	0	
				Mediators	Vegetation	Wspruce	0.002	0	0.001	0.003	*
						Bspruce	-0.005	0.11	-0.01	-0	*
						Birch	0	0	0	0	
						Poplars	-0.001	0	-0	0	
				Total	Climate	MSP	-0.014	0.05	-0.03	0.001	
						CMI	0.01	0.09	0	0.021	
						DD5	-0.004	0.05	-0.02	0.007	
						Tmin	-0.004	0.09	-0.01	-0	*
					Forest Structure	NDVI	0.017	0.01	0.007	0.027	*
						Psize	-0.048	0.01	-0.08	-0.02	*
						WetProb	-0.002	0.01	-0.02	0.026	
						Age	-0.015	0.01	-0.03	-0	*
						Cclosure	0.011	0.01	-0.01	0.035	
					Soil	tclay	-0.001	0.51	-0	0	
						tsand	0	0.42	-0	0	
					Vegetation	Wspruce	0.048	0.02	0.021	0.083	*
						Bspruce	0.038	0.01	0.018	0.057	*
						Birch	-0.002	0.01	-0.01	0.011	
						Poplars	-0.009	0	-0.01	-0.01	*

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Coniferous-associated (cont.)	BOCH	Boreal Chickadee	*Poecile hudsonicus*	**Direct**	Climate	MSP	0.001	0.01	-0.01	0.016	
						CMI	0.004	0.01	-0.01	0.02	
						DD5	0.007	0.01	-0.01	0.023	
					Forest Structure	NDVI	-0.006	0.01	-0.02	0.009	
						Psize	0.023	0.01	0.004	0.042	*
						WetProb	0.011	0.01	-0.01	0.031	
						Age	-0.004	0.01	-0.02	0.014	
						Cclosure	-0.005	0.01	-0.02	0.015	
					Vegetation	Wspruce	0.029	0.01	0.008	0.05	*
						Bspruce	0.037	0.01	0.017	0.056	*
						Birch	-0.033	0.01	-0.05	-0.01	*
						Poplars	0.016	0.02	0.004	0.066	*
				Indirect	Climate	MSP	0.001	0.06	-0	0.004	
						CMI	0.004	0.09	0.001	0.007	*
						DD5	-0.003	0.05	-0.01	0	
						Tmin	-0.003	0.08	-0.01	-0	*
					Soil	tclay	-0.002	0.66	-0	0	
						tsand	-0.001	0.55	-0	0	
				Mediators	Vegetation	Wspruce	0.001	0	0	0.002	
						Bspruce	-0.005	0.11	-0.01	-0	*
						Birch	-0.002	0	-0	-0	*
						Poplars	0.002	0	0	0.007	
				Total	Climate	MSP	0.002	0.06	-0.01	0.017	
						CMI	0.008	0.09	-0.01	0.023	
						DD5	0.005	0.06	-0.01	0.02	
						Tmin	-0.003	0.08	-0.01	-0	*
					Forest Structure	NDVI	-0.006	0.01	-0.02	0.009	
						Psize	0.023	0.01	0.004	0.042	*
						WetProb	0.011	0.01	-0.01	0.031	
						Age	-0.004	0.01	-0.02	0.014	
						Cclosure	-0.005	0.01	-0.02	0.015	
					Soil	tclay	-0.002	0.66	-0	0	
						tsand	-0.001	0.55	-0	0	
					Vegetation	Wspruce	0.029	0.01	0.008	0.05	*
						Bspruce	0.037	0.01	0.017	0.056	*
						Birch	-0.033	0.01	-0.05	-0.01	*
						Poplars	0.016	0.02	0.004	0.066	*

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Coniferous-associated (cont.)	GCKI	Golden-crowned Kinglet	*Regulus satrapa*	**Direct**	Climate	MSP	0.03	0.01	0.01	0.05	*
						CMI	0.025	0.01	0.011	0.04	*
						DD5	-0.021	0.01	-0.04	-0.01	*
					Forest Structure	NDVI	-0.064	0.01	-0.08	-0.05	*
						Psize	-0.032	0.01	-0.05	-0.02	*
						WetProb	-0.016	0.01	-0.03	0	
						Age	0.007	0.01	-0.01	0.029	
						Cclosure	0.023	0.01	0.009	0.039	*
					Vegetation	Wspruce	0.038	0.01	0.013	0.063	*
						Bspruce	0.014	0.01	-0	0.032	
						Birch	0.008	0.01	-0.01	0.032	
						Poplars	-0.029	0.01	-0.05	-0.01	*
				Indirect	Climate	MSP	-0.002	0.03	-0	-0	*
						CMI	0.005	0.01	0.001	0.008	*
						DD5	-0.003	0.04	-0.01	-0	*
						Tmin	-0.002	0.01	-0	0	
					Soil	tclay	-0.001	0.07	-0	0.001	
						tsand	0	0.06	0	0.001	
				Mediators	Vegetation	Wspruce	0.001	0	0	0.003	
						Bspruce	-0.002	0.06	-0	0	
						Birch	0	0	0	0.002	
						Poplars	-0.003	0	-0.01	-0	*
				Total	Climate	MSP	0.028	0.03	0.008	0.047	*
						CMI	0.03	0.01	0.016	0.045	*
						DD5	-0.024	0.04	-0.04	-0.01	*
						Tmin	-0.002	0.01	-0	0	
					Forest Structure	NDVI	-0.064	0.01	-0.08	-0.05	*
						Psize	-0.032	0.01	-0.05	-0.02	*
						WetProb	-0.016	0.01	-0.03	0	
						Age	0.007	0.01	-0.01	0.029	
						Cclosure	0.023	0.01	0.009	0.039	*
					Soil	tclay	-0.001	0.07	-0	0.001	
						tsand	0	0.06	0	0.001	
					Vegetation	Wspruce	0.038	0.01	0.013	0.063	*
						Bspruce	0.014	0.01	-0	0.032	
						Birch	0.008	0.01	-0.01	0.032	
						Poplars	-0.029	0.01	-0.05	-0.01	*

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Coniferous-associated (cont.)	MAWA	Magnolia Warbler	*Dendroica magnolia*	**Direct**	Climate	MSP	-0.022	0.01	-0.03	-0.01	*
						CMI	0.048	0.01	0.037	0.059	*
						DD5	-0.048	0.01	-0.06	-0.04	*
					Forest Structure	NDVI	0.007	0.01	-0.01	0.018	
						Psize	-0.007	0.01	-0.02	0.007	
						WetProb	0.02	0.01	0.007	0.034	*
						Age	0.004	0.01	-0.01	0.015	
						Cclosure	-0.017	0.01	-0.03	-0	*
					Vegetation	Wspruce	-0.009	0.01	-0.02	0.004	
						Bspruce	-0.005	0.01	-0.02	0.009	
						Birch	0.005	0.01	-0.01	0.021	
						Poplars	-0.011	0	-0.02	-0.01	*
				Indirect	Climate	MSP	-0.001	0.02	-0	0	
						CMI	-0.001	0	-0	0.002	
						DD5	0	0.01	-0	0.002	
						Tmin	0.001	0	0	0.002	
					Soil	tclay	0	0.15	-0	0.001	
						tsand	0	0.13	0	0.001	
				Mediators	Vegetation	Wspruce	0	0	-0	0	
						Bspruce	0.001	0.02	-0	0.002	
						Birch	0	0	0	0.001	
						Poplars	-0.001	0	-0	-0	*
				Total	Climate	MSP	-0.023	0.02	-0.03	-0.01	*
						CMI	0.047	0.01	0.037	0.058	*
						DD5	-0.048	0.01	-0.06	-0.04	*
						Tmin	0.001	0	0	0.002	
					Forest Structure	NDVI	0.007	0.01	-0.01	0.018	
						Psize	-0.007	0.01	-0.02	0.007	
						WetProb	0.02	0.01	0.007	0.034	*
						Age	0.004	0.01	-0.01	0.015	
						Cclosure	-0.017	0.01	-0.03	-0	*
					Soil	tclay	0	0.15	-0	0.001	
						tsand	0	0.13	0	0.001	
					Vegetation	Wspruce	-0.009	0.01	-0.02	0.004	
						Bspruce	-0.005	0.01	-0.02	0.009	
						Birch	0.005	0.01	-0.01	0.021	
						Poplars	-0.011	0	-0.02	-0.01	*

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Coniferous-associated (cont.)	SWTH	Swainson's Thrush	*Catharus ustulatus*	**Direct**	Climate	MSP	-0.006	0	-0.01	0	
						CMI	0.011	0	0.004	0.018	*
						DD5	-0.001	0	-0.01	0.005	
					Forest Structure	NDVI	0.017	0	0.01	0.023	*
						Psize	-0.01	0	-0.02	-0	*
						WetProb	0.008	0	0.002	0.015	*
						Age	0.027	0	0.021	0.034	*
						Cclosure	0.032	0	0.026	0.039	*
					Vegetation	Wspruce	0.01	0	0.005	0.015	*
						Bspruce	0.011	0	0.005	0.017	*
						Birch	0.005	0	-0	0.01	
						Poplars	-0.004	0	-0.01	0.001	
				Indirect	Climate	MSP	-0.001	0.03	-0	0	
						CMI	0.002	0.01	0.001	0.003	*
						DD5	-0.001	0.04	-0	-0	*
						Tmin	-0.001	0	-0	0	
					Soil	tclay	0	0.17	-0	0	
						tsand	0	0.14	0	0	
				Mediators	Vegetation	Wspruce	0	0	0	0.001	
						Bspruce	-0.001	0.06	-0	-0	*
						Birch	0	0	0	0	
						Poplars	0	0	-0	0	
				Total	Climate	MSP	-0.006	0.03	-0.01	-0	*
						CMI	0.013	0.01	0.007	0.02	*
						DD5	-0.003	0.04	-0.01	0.004	
						Tmin	-0.001	0	-0	0	
					Forest Structure	NDVI	0.017	0	0.01	0.023	*
						Psize	-0.01	0	-0.02	-0	*
						WetProb	0.008	0	0.002	0.015	*
						Age	0.027	0	0.021	0.034	*
						Cclosure	0.032	0	0.026	0.039	*
					Soil	tclay	0	0.17	-0	0	
						tsand	0	0.14	0	0	
					Vegetation	Wspruce	0.01	0	0.005	0.015	*
						Bspruce	0.011	0	0.005	0.017	*
						Birch	0.005	0	-0	0.01	
						Poplars	-0.004	0	-0.01	0.001	

Nesting Habitat	**Spp.**	**Eng. Name**	**Sci. Name**	**Effect Type**	**Var. Type**	**Variable**	**Effect**	**SE**	**L CI**	**U CI**	**Sig.**
Coniferous-associated (cont.)	WWCR	White-winged Crossbill	*Loxia leucoptera*	**Direct**	Climate	MSP	-0.011	0.01	-0.02	0.012	
						CMI	0.022	0.01	0.005	0.037	*
						DD5	-0.018	0.01	-0.03	-0	*
					Forest Structure	NDVI	-0.027	0.01	-0.04	-0.01	*
						Psize	-0.042	0.01	-0.06	-0.02	*
						WetProb	-0.006	0.01	-0.02	0.015	
						Age	-0.003	0.01	-0.02	0.014	
						Cclosure	0.029	0.01	0.01	0.047	*
					Vegetation	Wspruce	0.037	0.01	0.019	0.055	*
						Bspruce	0.075	0.01	0.055	0.096	*
						Birch	-0.009	0.01	-0.02	0.01	
						Poplars	-0.003	0	-0.01	0.001	
				Indirect	Climate	MSP	-0.002	0.24	-0	-0	*
						CMI	0.011	0.07	0.008	0.014	*
						DD5	-0.007	0.29	-0.01	-0.01	*
						Tmin	-0.006	0.03	-0.01	-0	*
					Soil	tclay	-0.003	1.11	-0	-0	*
						tsand	-0.001	0.92	-0	-0	*
				Mediators	Vegetation	Wspruce	0.001	0	0.001	0.002	*
						Bspruce	-0.01	0.45	-0.01	-0.01	*
						Birch	0	0	-0	0	
						Poplars	0	0	-0	0	
				Total	Climate	MSP	-0.013	0.24	-0.03	0.007	
						CMI	0.032	0.07	0.017	0.046	*
						DD5	-0.025	0.29	-0.04	-0.01	*
						Tmin	-0.006	0.03	-0.01	-0	*
					Forest Structure	NDVI	-0.027	0.01	-0.04	-0.01	*
						Psize	-0.042	0.01	-0.06	-0.02	*
						WetProb	-0.006	0.01	-0.02	0.015	
						Age	-0.003	0.01	-0.02	0.014	
						Cclosure	0.029	0.01	0.01	0.047	*
					Soil	tclay	-0.003	1.11	-0	-0	*
						tsand	-0.001	0.92	-0	-0	*
					Vegetation	Wspruce	0.037	0.01	0.019	0.055	*
						Bspruce	0.075	0.01	0.055	0.096	*
						Birch	-0.009	0.01	-0.02	0.01	
						Poplars	-0.003	0	-0.01	0.001	

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Coniferous-associated (cont.)	YRWA	Yellow-rumped Warbler	*Setophaga coronata*	**Direct**	Climate	MSP	-0.025	0	-0.03	-0.02	*
						CMI	0.032	0	0.025	0.039	*
						DD5	-0.042	0	-0.05	-0.04	*
					Forest Structure	NDVI	-0.016	0	-0.02	-0.01	*
						Psize	0.009	0	0.003	0.016	*
						WetProb	0.011	0	0.006	0.016	*
						Age	0.009	0	0.002	0.016	*
						Cclosure	0.021	0	0.013	0.028	*
					Vegetation	Wspruce	0.011	0	0.004	0.017	*
						Bspruce	0.031	0	0.024	0.037	*
						Birch	-0.008	0	-0.02	-0	*
						Poplars	0.003	0	-0.01	0.01	
				Indirect	Climate	MSP	-0.001	0.09	-0	0	
						CMI	0.004	0.02	0.003	0.005	*
						DD5	-0.003	0.1	-0	-0	*
						Tmin	-0.002	0.01	-0	-0	*
					Soil	tclay	-0.001	0.53	-0	-0	*
						tsand	-0.001	0.44	-0	0	
				Mediators	Vegetation	Wspruce	0	0	0	0.001	
						Bspruce	-0.004	0.15	-0.01	-0	*
						Birch	0	0	-0	0	
						Poplars	0	0	0	0.001	
				Total	Climate	MSP	-0.025	0.09	-0.03	-0.02	*
						CMI	0.036	0.02	0.029	0.043	*
						DD5	-0.045	0.1	-0.05	-0.04	*
						Tmin	-0.002	0.01	-0	-0	*
					Forest Structure	NDVI	-0.016	0	-0.02	-0.01	*
						Psize	0.009	0	0.003	0.016	*
						WetProb	0.011	0	0.006	0.016	*
						Age	0.009	0	0.002	0.016	*
						Cclosure	0.021	0	0.013	0.028	*
					Soil	tclay	-0.001	0.53	-0	-0	*
						tsand	-0.001	0.44	-0	0	
					Vegetation	Wspruce	0.011	0	0.004	0.017	*
						Bspruce	0.031	0	0.024	0.037	*
						Birch	-0.008	0	-0.02	-0	*
						Poplars	0.003	0	-0.01	0.01	

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Deciduous-associated	CAWA	Canada Warbler	*Wilsonia canadensis*	**Direct**	Climate	MSP	0.002	0.01	-0.01	0.011	
						CMI	-0.011	0.01	-0.02	0	
						DD5	0.013	0.01	0.001	0.025	*
					Forest Structure	NDVI	0.02	0.01	0.009	0.031	*
						Psize	-0.036	0.01	-0.05	-0.03	*
						WetProb	0	0	-0.01	0.007	
						Age	-0.004	0.01	-0.02	0.01	
						Cclosure	0.034	0.01	0.021	0.049	*
					Vegetation	Wspruce	-0.019	0.01	-0.03	-0	*
						Bspruce	-0.021	0.01	-0.03	-0.01	*
						Birch	0.018	0.01	0.003	0.039	*
						Poplars	0.003	0.01	-0.01	0.037	
				Indirect	Climate	MSP	0	0.03	-0	0.002	
						CMI	-0.003	0.07	-0.01	-0	*
						DD5	0.002	0.03	0.001	0.003	*
						Tmin	0.002	0.06	0.001	0.003	*
					Soil	tclay	0.001	0.38	0	0.003	
						tsand	0	0.31	0	0.001	
				Mediators	Vegetation	Wspruce	-0.001	0	-0	0	
						Bspruce	0.003	0.08	0.001	0.004	*
						Birch	0.001	0	0	0.002	
						Poplars	0	0	-0	0.003	
				Total	Climate	MSP	0.003	0.04	-0.01	0.011	
						CMI	-0.014	0.07	-0.03	-0	*
						DD5	0.015	0.04	0.004	0.026	*
						Tmin	0.002	0.06	0.001	0.003	*
					Forest Structure	NDVI	0.02	0.01	0.009	0.031	*
						Psize	-0.036	0.01	-0.05	-0.03	*
						WetProb	0	0	-0.01	0.007	
						Age	-0.004	0.01	-0.02	0.01	
						Cclosure	0.034	0.01	0.021	0.049	*
					Soil	tclay	0.001	0.38	0	0.003	
						tsand	0	0.31	0	0.001	
					Vegetation	Wspruce	-0.019	0.01	-0.03	-0	*
						Bspruce	-0.021	0.01	-0.03	-0.01	*
						Birch	0.018	0.01	0.003	0.039	*
						Poplars	0.003	0.01	-0.01	0.037	

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Deciduous-associated (cont.)	REVI	Red-eyed Vireo	*Vireo olivaceus*	**Direct**	Climate	MSP	0.009	0	0.004	0.015	*
						CMI	0.001	0	-0.01	0.007	
						DD5	0.007	0	0.001	0.014	*
					Forest Structure	NDVI	0.045	0	0.037	0.052	*
						Psize	0.008	0	0.001	0.016	*
						WetProb	0.006	0	-0	0.013	
						Age	0.001	0	-0.01	0.008	
						Cclosure	0.02	0	0.013	0.026	*
					Vegetation	Wspruce	-0.03	0	-0.04	-0.02	*
						Bspruce	-0.051	0.01	-0.06	-0.04	*
						Birch	-0.005	0	-0.01	0.001	
						Poplars	0.01	0	0.006	0.013	*
				Indirect	Climate	MSP	0.002	0.13	0.001	0.003	*
						CMI	-0.008	0.04	-0.01	-0.01	*
						DD5	0.006	0.16	0.005	0.007	*
						Tmin	0.004	0.02	0.003	0.005	*
					Soil	tclay	0.002	0.64	0.001	0.003	*
						tsand	0.001	0.54	0	0.001	
				Mediators	Vegetation	Wspruce	-0.001	0	-0	-0	*
						Bspruce	0.006	0.24	0.005	0.008	*
						Birch	0	0	-0	0	
						Poplars	0.001	0	0.001	0.001	*
				Total	Climate	MSP	0.011	0.13	0.006	0.017	*
						CMI	-0.007	0.04	-0.01	-0	*
						DD5	0.013	0.16	0.007	0.019	*
						Tmin	0.004	0.02	0.003	0.005	*
					Forest Structure	NDVI	0.045	0	0.037	0.052	*
						Psize	0.008	0	0.001	0.016	*
						WetProb	0.006	0	-0	0.013	
						Age	0.001	0	-0.01	0.008	
						Cclosure	0.02	0	0.013	0.026	*
					Soil	tclay	0.002	0.64	0.001	0.003	*
						tsand	0.001	0.54	0	0.001	
					Vegetation	Wspruce	-0.03	0	-0.04	-0.02	*
						Bspruce	-0.051	0.01	-0.06	-0.04	*
						Birch	-0.005	0	-0.01	0.001	
						Poplars	0.01	0	0.006	0.013	*

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Wetland-associated	ALFL	Alder Flycatcher	*Empidonax alnorum*	**Direct**	Climate	MSP	-0.018	0	-0.03	-0.01	*
						CMI	0.041	0.01	0.032	0.05	*
						DD5	-0.041	0	-0.05	-0.03	*
					Forest Structure	NDVI	0.015	0	0.006	0.023	*
						Psize	-0.009	0.01	-0.02	0	
						WetProb	0.017	0	0.009	0.026	*
						Age	-0.004	0	-0.01	0.005	
						Cclosure	-0.029	0.01	-0.04	-0.02	*
					Vegetation	Wspruce	-0.016	0	-0.02	-0.01	*
						Bspruce	0.004	0.01	-0.01	0.014	
						Birch	-0.011	0	-0.02	-0	*
						Poplars	0.004	0	-0	0.012	
				Indirect	Climate	MSP	0	0	-0	0.001	
						CMI	-0.001	0.01	-0	0	
						DD5	0	0	-0	0.001	
						Tmin	0	0.01	0	0.001	
					Soil	tclay	-0.001	0.04	-0	0	
						tsand	0	0.03	-0	0	
				Mediators	Vegetation	Wspruce	-0.001	0	-0	0	
						Bspruce	0	0.01	-0	0.001	
						Birch	-0.001	0	-0	0	
						Poplars	0	0	0	0.001	
				Total	Climate	MSP	-0.018	0.01	-0.03	-0.01	*
						CMI	0.04	0.01	0.031	0.048	*
						DD5	-0.041	0.01	-0.05	-0.03	*
						Tmin	0	0.01	0	0.001	
					Forest Structure	NDVI	0.015	0	0.006	0.023	*
						Psize	-0.009	0.01	-0.02	0	
						WetProb	0.017	0	0.009	0.026	*
						Age	-0.004	0	-0.01	0.005	
						Cclosure	-0.029	0.01	-0.04	-0.02	*
					Soil	tclay	-0.001	0.04	-0	0	
						tsand	0	0.03	-0	0	
					Vegetation	Wspruce	-0.016	0	-0.02	-0.01	*
						Bspruce	0.004	0.01	-0.01	0.014	
						Birch	-0.011	0	-0.02	-0	*
						Poplars	0.004	0	-0	0.012	

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Wetland-associated (cont.)	LISP	Lincoln's Sparrow	*Melospiza lincolnii*	**Direct**	Climate	MSP	-0.022	0	-0.03	-0.01	*
						CMI	0.044	0	0.036	0.052	*
						DD5	-0.04	0	-0.05	-0.03	*
					Forest Structure	NDVI	0.023	0	0.016	0.031	*
						Psize	0	0	-0.01	0.008	
						WetProb	0.022	0	0.016	0.029	*
						Age	0.004	0	-0	0.012	
						Cclosure	-0.044	0	-0.05	-0.04	*
					Vegetation	Wspruce	-0.011	0	-0.02	-0	*
						Bspruce	0.022	0	0.014	0.029	*
						Birch	-0.006	0	-0.01	0.003	
						Poplars	0	0.01	-0.01	0.008	
				Indirect	Climate	MSP	-0.001	0.06	-0	0	
						CMI	0.002	0.02	0	0.003	
						DD5	-0.002	0.08	-0	-0	*
						Tmin	-0.001	0.01	-0	0	
					Soil	tclay	-0.002	0.21	-0	-0	*
						tsand	0	0.17	-0	0	
				Mediators	Vegetation	Wspruce	0	0	-0	0	
						Bspruce	-0.003	0.12	-0	-0	*
						Birch	0	0	-0	0	
						Poplars	0	0	-0	0.001	
				Total	Climate	MSP	-0.023	0.06	-0.03	-0.01	*
						CMI	0.046	0.02	0.038	0.053	*
						DD5	-0.042	0.08	-0.05	-0.04	*
						Tmin	-0.001	0.01	-0	0	
					Forest Structure	NDVI	0.023	0	0.016	0.031	*
						Psize	0	0	-0.01	0.008	
						WetProb	0.022	0	0.016	0.029	*
						Age	0.004	0	-0	0.012	
						Cclosure	-0.044	0	-0.05	-0.04	*
					Soil	tclay	-0.002	0.21	-0	-0	*
						tsand	0	0.17	-0	0	
					Vegetation	Wspruce	-0.011	0	-0.02	-0	*
						Bspruce	0.022	0	0.014	0.029	*
						Birch	-0.006	0	-0.01	0.003	
						Poplars	0	0.01	-0.01	0.008	

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Wetland-associated (cont.)	NOWA	Northern Waterthrush	*Seiurus noveboracensis*	**Direct**	Climate	MSP	-0.001	0	-0.01	0.007	
						CMI	-0.002	0.01	-0.02	0.01	
						DD5	0.006	0.01	-0.01	0.019	
					Forest Structure	NDVI	0.016	0.01	0.005	0.026	*
						Psize	-0.01	0.01	-0.02	0.002	
						WetProb	0.016	0.01	0.001	0.033	*
						Age	-0.008	0.01	-0.02	0.004	
						Cclosure	0.002	0.01	-0.01	0.017	
					Vegetation	Wspruce	-0.004	0.01	-0.01	0.005	
						Bspruce	0.02	0.01	0.008	0.033	*
						Birch	0	0.01	-0.01	0.02	
						Poplars	0.001	0.01	-0.01	0.03	
				Indirect	Climate	MSP	-0.001	0.05	-0	0	
						CMI	0.002	0.01	0	0.004	
						DD5	-0.002	0.05	-0	0	
						Tmin	-0.001	0.01	-0	0	
					Soil	tclay	-0.001	0.29	-0	0	
						tsand	0	0.25	-0	0	
				Mediators	Vegetation	Wspruce	0	0	-0	0	
						Bspruce	-0.003	0.08	-0	-0	*
						Birch	0	0	0	0.001	
						Poplars	0	0	0	0.003	
				Total	Climate	MSP	-0.002	0.05	-0.01	0.006	
						CMI	0	0.01	-0.01	0.012	
						DD5	0.004	0.05	-0.01	0.017	
						Tmin	-0.001	0.01	-0	0	
					Forest Structure	NDVI	0.016	0.01	0.005	0.026	*
						Psize	-0.01	0.01	-0.02	0.002	
						WetProb	0.016	0.01	0.001	0.033	*
						Age	-0.008	0.01	-0.02	0.004	
						Cclosure	0.002	0.01	-0.01	0.017	
					Soil	tclay	-0.001	0.29	-0	0	
						tsand	0	0.25	-0	0	
					Vegetation	Wspruce	-0.004	0.01	-0.01	0.005	
						Bspruce	0.02	0.01	0.008	0.033	*
						Birch	0	0.01	-0.01	0.02	
						Poplars	0.001	0.01	-0.01	0.03	

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Wetland-associated (cont.)	TEWA	Tennessee Warbler	*Vermivora peregrina*	**Direct**	Climate	MSP	-0.031	0	-0.04	-0.02	*
						CMI	0.051	0	0.045	0.058	*
						DD5	-0.06	0	-0.07	-0.05	*
					Forest Structure	NDVI	0.001	0	-0.01	0.008	
						Psize	-0.004	0	-0.01	0.003	
						WetProb	-0.02	0	-0.03	-0.01	*
						Age	0.019	0	0.012	0.026	*
						Cclosure	-0.01	0	-0.02	-0	*
					Vegetation	Wspruce	0	0	-0.01	0.006	
						Bspruce	0.014	0	0.007	0.021	*
						Birch	0.002	0	-0.01	0.009	
						Poplars	-0.012	0.01	-0.02	0	
				Indirect	Climate	MSP	-0.001	0.05	-0	-0	*
						CMI	0.002	0.01	0.001	0.003	*
						DD5	-0.002	0.06	-0	-0	*
						Tmin	-0.001	0.01	-0	0	
					Soil	tclay	-0.001	0.25	-0	0	
						tsand	0	0.21	0	0	
				Mediators	Vegetation	Wspruce	0	0	0	0	
						Bspruce	-0.002	0.09	-0	-0	*
						Birch	0	0	0	0	
						Poplars	-0.001	0	-0	0	
				Total	Climate	MSP	-0.032	0.05	-0.04	-0.03	*
						CMI	0.053	0.01	0.047	0.06	*
						DD5	-0.062	0.06	-0.07	-0.06	*
						Tmin	-0.001	0.01	-0	0	
					Forest Structure	NDVI	0.001	0	-0.01	0.008	
						Psize	-0.004	0	-0.01	0.003	
						WetProb	-0.02	0	-0.03	-0.01	*
						Age	0.019	0	0.012	0.026	*
						Cclosure	-0.01	0	-0.02	-0	*
					Soil	tclay	-0.001	0.25	-0	0	
						tsand	0	0.21	0	0	
					Vegetation	Wspruce	0	0	-0.01	0.006	
						Bspruce	0.014	0	0.007	0.021	*
						Birch	0.002	0	-0.01	0.009	
						Poplars	-0.012	0.01	-0.02	0	

Nesting Habitat	Spp.	Eng. Name	Sci. Name	Effect Type	Var. Type	Variable	Effect	SE	L CI	U CI	Sig.
Wetland-associated (cont.)	WIWA	Wilson's Warbler	*Wilsonia pusilla*	**Direct**	Climate	MSP	-0.027	0.01	-0.05	-0.01	*
						CMI	0.032	0.01	0.013	0.049	*
						DD5	-0.025	0.01	-0.04	-0.01	*
					Forest Structure	NDVI	0.005	0.01	-0.01	0.023	
						Psize	-0.002	0.01	-0.03	0.022	
						WetProb	0.039	0.02	0.008	0.075	*
						Age	0.005	0.01	-0.01	0.023	
						Cclosure	-0.03	0.01	-0.05	-0.01	*
					Vegetation	Wspruce	-0.004	0.01	-0.02	0.014	
						Bspruce	0.024	0.01	-0	0.052	
						Birch	0.029	0.02	-0	0.086	
						Poplars	-0.008	0	-0.01	-0	*
				Indirect	Climate	MSP	-0.002	0.09	-0	-0	*
						CMI	0.004	0.03	0	0.009	
						DD5	-0.003	0.11	-0.01	0	
						Tmin	-0.001	0.01	-0	0.001	
					Soil	tclay	0	0.52	-0	0.002	
						tsand	0	0.44	-0	0	
				Mediators	Vegetation	Wspruce	0	0	-0	0.001	
						Bspruce	-0.003	0.17	-0.01	0	
						Birch	0.001	0	0	0.004	
						Poplars	-0.001	0	-0	0	
				Total	Climate	MSP	-0.029	0.09	-0.05	-0.01	*
						CMI	0.036	0.03	0.021	0.051	*
						DD5	-0.028	0.11	-0.04	-0.01	*
						Tmin	-0.001	0.01	-0	0.001	
					Forest Structure	NDVI	0.005	0.01	-0.01	0.023	
						Psize	-0.002	0.01	-0.03	0.022	
						WetProb	0.039	0.02	0.008	0.075	*
						Age	0.005	0.01	-0.01	0.023	
						Cclosure	-0.03	0.01	-0.05	-0.01	*
					Soil	tclay	0	0.52	-0	0.002	
						tsand	0	0.44	-0	0	
					Vegetation	Wspruce	-0.004	0.01	-0.02	0.014	
						Bspruce	0.024	0.01	-0	0.052	
						Birch	0.029	0.02	-0	0.086	
						Poplars	-0.008	0	-0.01	-0	*