

A climatic basis for microrefugia: the influence of terrain on climate

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Abstract

There is compelling evidence from glacial and interglacial periods of the Quaternary of the utilization of microrefugia. Microrefugia are sites that support locally favorable climates amidst unfavorable regional climates, which allow populations of species to persist outside of their main distributions. Knowledge of the location of microrefugia has important implications for climate change research as it will influence our understanding of the spatial distribution of species through time, their patterns of genetic diversity, and potential dispersal rates in response to climate shifts. Indeed, the implications of microrefugia are profound and yet we know surprisingly little about their climatic basis; what climatic processes can support their subsistence, where they may occur, their climatic traits, and the relevance of these locations for climate change research. Here I examine the climatic basis for microrefugia and assert that the interaction between regional advective influences and local terrain influences will define the distribution and nature of microrefugia. I review the climatic processes that can support their subsistence and from this climatic basis: (1) infer traits of the spatial distribution of microrefugia and how this may change through time; (2) review assertions about their landscape position and what it can tell us about regional climates; and (3) demonstrate an approach to forecasting where microrefugia may occur in the future. This synthesis highlights the importance of landscape physiography in shaping the adaptive response of biota to climate change.

Keywords: climate change, cryptic refugia, landscape physiography, microrefugia, mountain climate, paleoclimate, refugia, species distributions, topoclimate

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Introduction

The response of biota to climate change of the past is pertinent to understanding present day biotic response to anthropogenic warming (Noss, 2001; Pearson, 2006; Provan & Bennet, 2008). One such adaptive response garnering increased attention is the purported utilization of climatic refugia by biota. Climatic refugia are typically thought of as large regions in which organisms took refuge during glacial advances and retreats during the Pleistocene (2.5 million years ago to 11 500 years ago), which then acted as sources for colonization during more favorable climatic periods (Hewitt, 2000; Davis & Shaw, 2001). Areas in Southern Europe (e.g. the Iberian Peninsula, Southern Italy, the Balkans) and regions of the southeastern US are widely accepted as climatic refugia for thermophilous species during the last glacial maximum (LGM; 18 000–25 000 years ago) (Hewitt, 2000; Jackson & Overpeck, 2000; Jackson *et al.*, 2000; Birks & Willis, 2008). In addition to these large-scale refugia, there is compelling evidence that climatic refugia occurred at *local* scales during the LGM and

were also utilized during interglacial warm periods, including the current interglacial (Willis & Van Andel, 2004; Birks & Willis, 2008). These ‘microrefugia’ or ‘cryptic refugia’ were sites that supported isolated low-density populations of species beyond their reconstructed range boundaries. It is hypothesized that these refugial habitats occurred in favorable microclimates during periods of unfavorable regional climate and allowed for postglacial colonization via local dispersal (McLachlan *et al.*, 2005; Pearson, 2006; Birks & Willis, 2008; Provan & Bennet, 2008).

The purported utilization of microrefugia has far-reaching implications for understanding adaptive and evolutionary responses of biota to climate shifts. For instance, the existence of microrefugia has evolutionary implications on the rates of genetic divergence within isolated populations under climate change (Hewitt, 2000; Stewart *et al.*, 2004). Additionally, microrefugia are viewed as a potential resolution to ‘Reid’s Paradox,’ the incongruence between estimated postglacial migration rates and tree dispersal capacity (Pearson, 2006). Their existence would suggest that long distance dispersal [leptokurtic dispersal (Clark *et al.*, 1998)] is not required to achieve rapid migrations and as such, is relevant to ongoing discussion about

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the dispersal capacity of species in response to anthropogenic warming.

Indeed, there are many implications of microrefugia and yet our understanding of them is quite limited. Most notably, we lack an understanding of the climatic basis for explaining their existence. Investigators commonly attribute their subsistence to the presence of 'microclimates,' and implicit assumption that spatial variation in climate can support microrefugia. Beyond this assumption, there is little explicit understanding of the climatic processes that would allow for microrefugia to exist. For instance, in a recent review, Rull (2009) states 'Their (microrefugia) precise characteristics, besides the also speculative but necessary occurrence of favorable microclimates, are unknown.' He goes on to describe microrefugia as a 'theoretical necessity without an appropriate biogeographical and ecological characterization' (Rull, 2009). This assessment is accurate. To my knowledge, there has been no systematic examination of what climatic processes can support the existence of microrefugia, where they might occur, their potential climatic traits, and the relevance of these locations for climate change research. An assessment such as this is critical to identifying microrefugia as well as for understanding proximal mechanisms by which organisms may respond to climate change.

This article will focus on understanding the climatic processes that can support the subsistence of microrefugia. Here I consider microrefugia to be defined by climate. Thus, I draw a distinction between the use of the term 'climatic refugia,' as used by Noss (2001) which describes sites that support unique biota due to *rare* edaphic or geomorphic conditions that can affect climate (e.g. alpine slopes), and my usage of the term microrefugia which characterizes *common* physiographic settings in landscapes that support climates (and potentially biological communities) that are disparate from their surroundings. Research in mountain climate and meteorology has noted that the climate experienced *in situ* is the sum of regional advective influences and local terrain influences (Pepin & Lundquist, 2008). I will review this research as it is relevant to identifying microrefugia. From this climatic basis, I: (1) infer traits of the spatial distribution of microrefugia, how this may change through time, and assess the relevance of the distribution of microrefugia to climate change research; (2) review assertions about the landscape position of microrefugia of the past and what it tells us about regional climates of the time; and (3) demonstrate an approach to forecast where microrefugia may occur in the future.

This article will focus principally on plant systems in mountain environments. Mountains support patchy habitat and contain steep climatic gradients making

them likely locations for microrefugia. Further, mountains support roughly one quarter of terrestrial biodiversity, contain 32% of protected areas and nearly half of the world's biodiversity hotspots (Körner & Ohsawa, 2005). Additionally, I focus on research in plant systems. Given their sessile nature, plants will presumably have a more apparent linkage to climate than animals. This will tend to reduce ambiguity in interpreting results of studies and lends itself to more direct interpretations of climate–organism responses.

A climatic basis for microrefugia

Microrefugia are areas that support locally favorable climates, in which populations of species can survive outside their main distribution, protected from regionally limiting climatic factors (adapted from Rull, 2009). Microrefugia support relict climates. More specifically, they should be found in physiographic settings that can support once prevalent regional climates that have been lost (or are being lost) due to climate shifts (Birks & Willis, 2008). This trait allows them to act as climatically *sui habitat* for species with previously more widespread distributions. Accordingly, to develop a climatic basis for microrefugia will require an understanding of: (1) the traits of regional climates and how they change over time (climate dynamics); (2) how regional climates limit the distribution of species (i.e. limiting climatic factors); and (3) the mechanisms by which terrain can moderate regionally limiting climates, as experienced *in situ*, thus allowing for species to persist locally.

Climate dynamics

Climate dynamics during the Quaternary are important to understanding the traits of microrefugia. Climate during the Quaternary has fluctuated between glacial periods that lasted on average 80 000 years, and interglacial periods that lasted on the order of 10 000 years. Thus, glacial-stage or 'cold period' conditions account for roughly 80% of the Quaternary, whereas the remainder consists of interglacial stages ('warm periods') in which conditions were similar to or potentially warmer than those today (Jackson & Overpeck, 2000). Regional climate reconstructions of the LGM suggest that high latitude areas (>40°N) had temperatures that were possibly 10–20 °C lower than today, whereas, lower latitude regions were significantly drier and had temperatures that were 2–5 °C lower than the present (Petit *et al.*, 1999; Barron & Pollard, 2002; Willis & Van Andel, 2004; Birks & Willis, 2008).

Sites that support microrefugia likely differed between glacial and interglacial stages. During interglacial stages, microrefugia were presumably found in areas

with cooler microclimates that allowed for the persistence of cold-adapted species. During the longer glacial stages, microrefugia presumably supported warm microclimates that allowed for the persistence of thermophilous species (Table 1) (Birks & Willis, 2008; Rull, 2009). In the current interglacial period, microrefugia are likely to have lower temperatures and support more mesic environments than their surroundings. These represent climatic environments that will become increasingly scarce in the next century due to anthropogenic warming (IPCC, 2007; Williams *et al.*, 2007). Additionally, warming over the past century has been asymmetric with minimum temperature increasing nearly twice as rapidly as maximum temperature (IPCC, 2007). At the regional scale, studies have reported an increase in minimum temperatures in the Sierra Nevada, USA (Dettinger & Cayan, 1995), the Rockies, USA (Brown *et al.*, 1992), the Swiss Alps (Beniston *et al.*, 1994) and a nominal increase in maximum temperature over a comparable time period. Because minimum temperature is rising at a greater rate than maximum temperature under anthropogenic warming, current, and future microrefugia are likely to support minimum temperature regimes of extant climates.

Limiting climatic factors

Knowledge of limiting climatic factors is important for identifying the physiographic mechanisms by which microrefugia can ameliorate climatic constraints on a species. These climatic constraints are likely to vary regionally. For example, in arid regions where water availability constrains species distributions, a locally moist site may act as a refugium. In contrast, at high latitudes, landscape positions that buffer against extreme minimum temperatures may act as refugia. Both sites provide refugial habitat but the climatic mechanisms by which they operate may be quite different in each case. Consequently, a regional context, and an understanding of limiting climatic factors, is important for assessing the mechanisms by which microrefugia allow species to subsist locally.

In this review, I focus on two climate factors that play a critical role in defining the distributions of species: temperature and climatic water balance. Climatic water balance is widely recognized as a critical driver of the distribution of plant physiognomic types at continental scales and species at local scales (Stephenson, 1998; Urban *et al.*, 2000; Lutz *et al.*, 2010). Similarly, temperature constrains species ranges for multiple taxa [e.g. insects (Tenow & Nilssen, 1990; Bale, 2002); plants (Woodward, 1987)]. For plants, this may operate through effects on adult individuals, and through its

Table 1 Summary of traits of microrefugia organized by glacial stage, limiting climatic factor, and species characteristics

Quaternary stage	Limiting climatic factor	Reference taxa	Physiologic or ecologic limiting mechanism	Refugial position	Topoclimatic mechanism
Glacial (cold period)	Minimum temperature	Thermophilous taxa	Growing season length/physical barrier due to snow and ice	South-facing slopes	Solar insolation effects on snow/ice pack duration
	Water availability	Mesophilous taxa	Water stress, desiccation	Convergent environments/north-facing slopes	Water accumulation/protection from wind and desiccation/lower evaporative demand
Interglacial (warm period)	Inadequate minimum temperature	Cold-adapted taxa	Competition from thermophilous taxa, disturbance due to inadequate minimum temperatures*	Convergent environments	Cold air pooling
	Maximum temperature	Cold-adapted taxa	High temperature stress, competition from thermophilous taxa	(Exclude south-facing aspects)	Solar insolation effect on maximum temperature
	Water availability	Mesophilous taxa	Water stress, desiccation	Convergent environments/north-facing slopes	Water accumulation/protection from wind and desiccation/lower evaporative demand

Limiting climatic factors are likely to vary by regional climatic traits. Convergent environments include valley bottoms, local depressions, sinks, and basins. *For example, inadequate minimum temperatures for overwintering mortality of insects (e.g. Tenow & Nilssen, 1990).

influence in defining the regeneration niche (Blennow & Lindkvist, 2000). In particular, minimum temperature profoundly influences the life history of species due to the ecological and evolutionary impacts of freezing (Inouye, 2000). For example, physiological research on the influence of climate change on plants has focused on adaptations to higher minimum temperatures, increased temperature variance, and trade-offs between utilizing the full growing season and minimizing frost damage through the timing of budbreak and hardening [reviewed by Saxe *et al.* (2001)].

Terrain effects on climate

The climate experienced by an organism *in situ* (and the climate of microrefugia) is the sum of regional advective influences and local terrain influences (Daly, 2006; Lundquist & Cayan, 2007; Daly *et al.*, 2009). This is known as topoclimate, a term that can be attributed to Thornthwaite (Thornthwaite, 1953) and refers to spatial estimates of climate as it varies with topographic position in the landscape (Weiss *et al.*, 1988; Brown, 1991). Other synonyms found in the literature include terrain climate, local climate, and mesoclimate (Geiger, 1965). Physiographic factors such as elevation, slope, aspect, and topographic convergence influence meteorological elements including air temperature, precipitation, wind, solar insolation, cold air drainage, evapotranspiration, snow accumulation, and melt (Thornthwaite, 1953; Weiss *et al.*, 1988; Brown, 1991; Coughlan & Running, 1997). Topoclimate is highly pertinent in climate change research because it, along with edaphic drivers, defines the physical template that organisms experience, and thus constrains habitat suitable for the growth, survival, and reproduction of organisms (Davis & Dozier, 1990; Brown, 1994; Urban *et al.*, 2000).

Terrain affects the level of coupling between the climate experienced *in situ* and regional climate patterns. Climate patterns can be defined by their current state (mean condition at a given location) as well as their dynamics (change over time or trend). For microrefugia to exist, terrain influences must allow for climate states that deviate from regional averages (i.e. allow for climates that are warmer, colder, wetter, and drier than regional averages). Similarly, for microrefugia to persist, they must decouple their climate trends from regional trends or else they will be short lived. Sites that are consistently decoupled from regional patterns are good candidates for microrefugia because they are more likely to support relict climates as compared with sites with strong coupling to the free-atmosphere, which tend to track regional climates. Here I draw attention to three terrain influences that affect the level of coupling between the boundary layer and

the free atmosphere, and drive local variation in air temperature and water balance: (1) cold air drainage, (2) elevation, and (3) slope and aspect effects. My objective is not to rigorously review the components of mountain climate [see (Geiger, 1965), (Barry, 1992) for a thorough treatment of this material] but rather to identify terrain features that can promote local climates that are effectively decoupled from regional climatic patterns, a requisite for the subsistence of microrefugia.

Cold air drainage and convergent environments. Terrain positions that consistently promote cold-air pooling and the maintenance of temperature inversions are primary candidates for microrefugia. This is because they represent landscape positions whose climatic environments are consistently decoupled from regional circulation patterns (Lundquist *et al.*, 2008; Daly *et al.*, 2009). These convergent environments have a key trait of extant climatic environments being lost today and climatic environments that were presumably lost during interglacial warm periods of the Pleistocene; consistently lower minimum temperatures (Geiger, 1965; Lookingbill & Urban, 2003; Daly *et al.*, 2009; Dobrowski *et al.*, 2009) (Fig. 1). Convergent environments (e.g. valley bottoms, local depressions, coves, sinks, basins, etc.) also accumulate water and soil (which helps retain water). Thus, they conceivably could act as microrefugia for mesophilous taxa in arid regions (Table 1).

Cold air pooling is a widespread phenomenon in areas of complex terrain. In the absence of strong winds, temperatures drop rapidly after sunset resulting in strong nocturnal cooling near the ground surface. Cold dense air drains into convergent environments, resulting in stable cold air pools that can be hundreds of meters thick (Lindkvist *et al.*, 2000; Whiteman *et al.*, 2004). This results in an increase in temperature with increasing elevation (inversion). Inversions are promoted by stable atmospheric conditions. In many cases, sites in topographic depressions (e.g. heavily incised valleys) are sheltered from regional advective influences. The lack of vertical mixing within these cold air pools decouples air within the inversion from the free atmosphere above (Whiteman, 1982; Whiteman *et al.*, 2004; Daly *et al.*, 2009).

Cold air pooling occurs frequently in basins, valleys, and sinks of mountainous regions. It has been documented to occur as often as 30–60% of the daily observations made in mountainous regions around the globe (Bolstad *et al.*, 1998; Iijima & Shinoda, 2000; Dobrowski *et al.*, 2007; Blandford *et al.*, 2008). Cold air pools are not solely nocturnal phenomena, but also influence diurnal temperature patterns. Researchers have demonstrated that inversions can last from 3 to 6 h past sunrise (Whiteman, 1982; Muller & Whiteman,

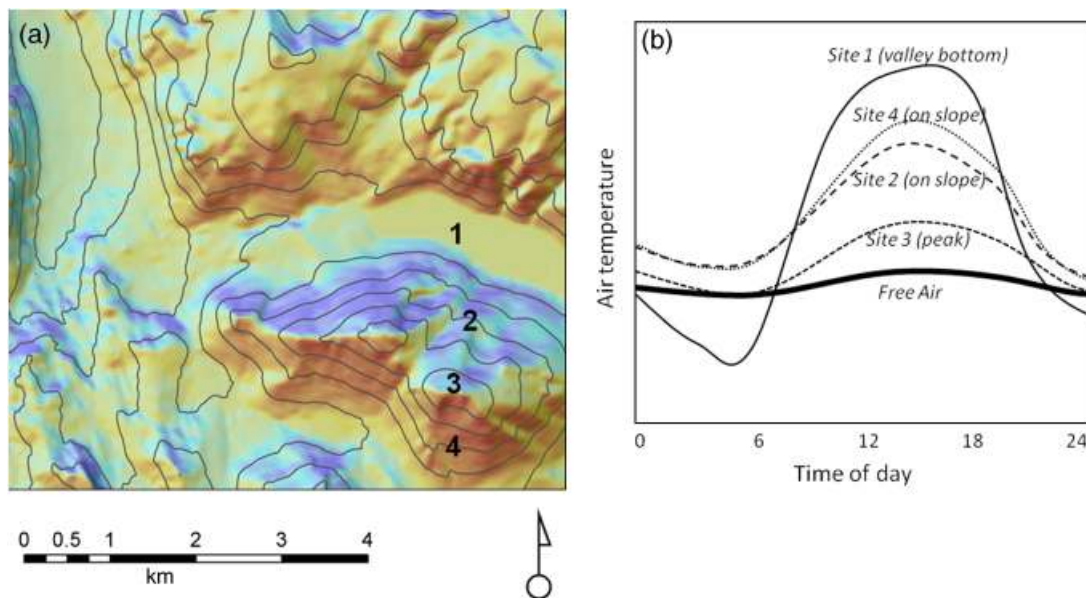


Fig. 1 Representation of the influence of landscape position on air temperature and diurnal temperature variance. (a) Shaded relief map shows areas of high (warm colors) and low (cool colors) solar insolation with the locations of four hypothetical sites. (b) Typical pattern of diurnal temperatures for sites 1–4 (adapted from Geiger, 1965). Site 3 (peak) shows the strongest coupling to the free-air environment and exhibits the smallest diurnal temperature variance. Site 1 (valley bottom) shows the weakest coupling to the free-air environment and exhibits both lower minimum temperatures and higher maximum temperatures than other sites. Site 4 occurs on the same elevation contour as site 2 and will potentially have higher maximum temperatures due to effects of enhanced solar insolation.

1988; Colette *et al.*, 2003). Moreover, the formation, break-up, and strength of inversions are strongly influenced by terrain configuration. The depth, width, and orientation of a valley influences the amount and timing of the solar insolation it receives and the amount of boundary layer mixing due to wind (Whiteman, 1982; Anquetin *et al.*, 1998; Colette *et al.*, 2003; Whiteman *et al.*, 2004).

There have been notable efforts modeling cold air drainage and its influence on temperature. Investigators have shown that minimum temperature estimates are greatly improved by using terrain variables that characterize surface water accumulation such as distance to streams, flow accumulation, or topographic convergence (Chung *et al.*, 2002; Lookingbill & Urban, 2003; Daly *et al.*, 2009; Dobrowski *et al.*, 2009) as these can act as proxies for cold-air drainage. Similarly, Lundquist *et al.* (2008) showed that terrain position could be classified as prone or not-prone to cold air pooling within study sites in the Rocky Mountains and Sierra Nevada, USA, and the Pyrenees of France. These studies and others have consistently demonstrated that modeling of minimum temperature requires terrain data as it pertains to the formation and maintenance of cold air pools.

Elevation as a predictor of microrefugia. Elevation is likely to be of limited use in identifying microrefugia because elevation unto itself is a poor predictor of the level

of coupling between the boundary layer and the free-atmosphere (Pepin & Norris, 2005; Pepin & Lundquist, 2008). In contrast, elevation *combined* with information on landscape position can be useful for identifying microrefugia. High elevation sites that are exposed and free-draining (e.g. mountain peaks) tend to have temperature variance that is more closely coupled to the free-air environment as compared with low elevation sites that are protected (Pepin & Seidel, 2005). This is due to a number of factors that influence the stability and depth of the boundary layer and the amount of mixing that occurs between it and the free atmosphere (Geiger, 1965; Pepin & Norris, 2005). As evidence of this, empirical observations demonstrate that mountain summits tend to have diurnal temperature ranges that more closely mirror that of the free-atmosphere (Fig. 1) (Geiger, 1965). In contrast, sheltered valley sites at lower elevations are likely to have less climatic coupling to the free air environment, stronger temperature differentials from regional averages (e.g. lower minimum temperatures due to strong decoupling of the surface and free-atmosphere which results in stable cold air pools), and greater diurnal temperature variance (Geiger, 1965; Lundquist *et al.*, 2008). These climatic processes help explain why temperatures within a region can vary dramatically at the same elevation depending on landscape position

(Lookingbill & Urban, 2003; Dobrowski *et al.*, 2009), and in particular, why elevation is a weak predictor of minimum temperature in areas of complex terrain (Lookingbill & Urban, 2003; Dobrowski *et al.*, 2009).

Slope and aspect effects on temperature and water balance. Slope and aspect influence near-surface temperature and water availability due to varying exposure to solar radiation and wind (McCutchan & Fox, 1986; Barry, 1992; Bolstad *et al.*, 1998). Solar radiation has been used as a predictor variable in modeling temperature in complex terrain (Geiger, 1965; Lookingbill & Urban, 2003; Chung & Yun, 2004; Dobrowski *et al.*, 2009; Fridley, 2009). However, many of these authors note that the effect of direct beam solar radiation is most pronounced on daily maximum temperatures and has little influence on minimum temperature. Further, this effect is strongly modified by cloud cover which diminishes radiation differences between exposures, as well as by high soil moisture or canopy cover which can shift the conversion of shortwave radiation to latent as opposed to sensible heat flux. Thus, the influence of slope and aspect on air temperature will be greater in arid sites and diminished in mesic sites (Fridley, 2009).

Comparatively, slope and aspect have a more marked effect on water balance than temperature. Reference evapotranspiration is affected by slope and aspect primarily through differences in shortwave radiation and wind exposure (Hupet & Vanclooster, 2001; Gong *et al.*, 2006; Mcvicar *et al.*, 2007). The influence of slope and aspect on the radiation environment is well understood (Geiger, 1965; Chung & Yun, 2004) whereas much less is known about the interaction between slope, aspect, and prevalent wind direction in landscape-scale modeling efforts [although see Ashcroft *et al.* (2009)]. Slope and aspect also influence snowmelt patterns. Coughlan & Running (1997) demonstrated that after canopy cover, net solar radiation is the most important factor affecting snowpack duration. This effect varies by elevation: low elevation snowpacks become isothermal earlier in the spring, experience greater insolation differences between hillslopes due to low solar angles earlier in the season, and thus have increased sensitivity to slope and aspect. High elevation snowpacks become isothermal later in the season when radiation differences between slope facets are less dependent on solar angles, thus diminishing the role of slope and aspect differences between sites (Coughlan & Running, 1997).

Given this background, we can posit that slope and aspect will play a greater role in shaping the location of microrefugia in arid regions as compared with regions in which temperature is limiting. This is because slope and aspect (which influence radiation and wind expo-

sure) arguably have a larger relative influence on water balance as compared with air temperature (Mcvicar *et al.*, 2007). Similarly, the effect of short-wave radiation on air temperature will be more pronounced in arid regions than mesic regions.

Can terrain effects on climate explain microrefugia? The importance of topoclimatic effects in defining microrefugia depends on the influence these terrain effects exert on *in situ* climate patterns. If terrain effects on climate patterns (state and trend) are small, then the plausibility of physiographically defined microrefugia is overstated. If these physiographic effects are large, then their importance has been overlooked. In the following section, I review relevant research in an attempt to address this question.

The influence of terrain on the climate state is pronounced and temporally variable. For example, the author (Dobrowski *et al.*, 2009) decomposed *in situ* temperature measurements into components associated with regional free-air temperature and local physiographic effects and found that roughly 20–30% of the temperature variance of a mountainous region over an 11 year period could be attributed to spatial variance in physiographic features. This influence is likely to be even greater at sites with pronounced topoclimatic effects. In the Great Smoky Mountains of the Eastern US, Fridley (2009) showed that topoclimatic effects resulted in 2–4 °C of *in situ* temperature variance, depending on the temperature variable (minimum or maximum), and time of year. In the Sierra Nevada, USA the author demonstrated that physiographic effects on climate can result in average temperature differences up to 5 °C during the winter months, minimum temperature differentials of 5–8 °C, and over a 20% difference in reference evapotranspiration between proximal sites at the same elevation (Dobrowski *et al.*, 2009). In a particularly relevant example, Daly *et al.*, (2009) demonstrates that topoclimatic modeling of cold-air pooling coupled with projected climate warming, can result in widely divergent temperature changes of up to 6 °C for proximal locations (<2 km) in mountainous terrain. These topoclimatic effects exceeded values of the imposed regional temperature change.

Terrain position can also decouple the climate trend a site experiences from regional trends. For example, using hundreds of historic temperature records in mountainous regions around the globe, Pepin and colleagues (2008; 2002; 2003; 2005) demonstrates that paired surface and free air temperature measurements have highly variable and sometimes conflicting temperature trends. Pepin & Lundquist (2008) further demonstrate that the variance in temperature trend magnitude (°C decade⁻¹) measured at mountain sites

over a 55-year period relates to their terrain position. Sites that exhibit strong coupling to the free-air environment (e.g. mountain summits) have low variance and temperature trends that closely track the free-air environment, and thus, are poor candidates for microrefugia. In contrast, sites with weak coupling to the free-atmosphere (e.g. valley bottom sites), have the largest variance in trend magnitude, exhibiting both warming and cooling trends [fig. 4c and d; (Pepin & Lundquist, 2008)]. Consequently, these sites have a greater potential to support temperature trends that deviate from regional averages and are more likely to be able to support relict climates through time.

Given the amplitude of the topoclimatic effects described above, physiographic effects, independent of elevation, could allow for the subsistence of species within microrefugia. The temperature differentials (described above) attributable to terrain are consistent with the estimated temperature differences between the LGM and current climate in lower latitude regions (2–5 °C) (Petit *et al.*, 1999; Barron & Pollard, 2002; Willis & Van Andel, 2004; Birks & Willis, 2008). Further, terrain position can influence the level of coupling between climate trends measured *in situ* and regional trends. Taken together, the capacity of local physiography to influence the climate state and trend is critical to understanding the climatic basis for microrefugia, and as described in the next section, will allow us to develop hypotheses about the spatial distribution of microrefugia through time.

Spatial and temporal distribution of microrefugia

The physiographic settings and climatic processes that can potentially support microrefugia are widespread in areas of complex terrain. Consequently, the utilization of microrefugia is likely to be an adaptive strategy that is widespread. Although the climatic processes that support microrefugia are common (e.g. cold-air drainage), their actual influence on *in situ* climate patterns will vary in degree and intensity depending on terrain position and regional climatic context. In other words, many locations in landscapes can act as microrefugia, but the extent to which they maintain relict climates will vary in degree and duration. Areas with pronounced topoclimatic effects that are consistently decoupled from regional climate patterns will maintain relict climates for longer durations than sites that are tightly coupled to the free-air environment. We can view this as a spectrum of terrain positions with varying degrees of coupling to the free atmosphere. Microrefugia that supported thermophilous taxa over long durations during the LGM lie on one end of this spectrum. On the opposite end of the spectrum are exposed high eleva-

tion sites, which have climates that are tightly coupled to the free atmosphere. In between these two extremes is most of the landscape.

Given this, we can posit that the utilization of microrefugia by species will vary in space as regional climates change (Fig. 2). Starting from a reference climate suitable for a given species, isolates are likely to be widely dispersed throughout an inhospitable region [*sensu* 'widespread and diffuse' microrefugia (Rull, 2009)]. As time passes and regional climate becomes less suitable for a given species, the number of microrefugia that can support a locally favorable climate for that species will decrease with those remaining becoming increasingly isolated. Further, climate gradients will result in a reduction in the number of microrefugia with increasing distance from the main distribution of the species (macrorefugium). The rate of decline will be dependent on the degree of climatic coupling that a site exhibits (Fig. 2b). Sites that are strongly coupled to the free-atmosphere will exhibit a maximal rate of decrease in the number of microrefugia with increasing distance from the macrorefugium, this rate being defined by the steepness of the underlying limiting climatic gradient. In contrast, a portion of the sites with weak coupling to regional conditions will be able to maintain isolates at greater distances from the macrorefugium because these isolates have a greater potential to persist at these sites through time.

There are a number of assumptions in this model that deserve examination. The first is that terrain position can result in sites with consistent climate deviations from regional averages. This contention has received much attention in this review and is well supported by research in climate science, meteorology, and landscape ecology. Another assumption is that terrain position can decouple the climate *trend* a site experiences from regional trends. There is compelling evidence for this contention as well (reviewed previously) although our understanding of why, for example, a mountain valley site would have a differential response to climate change as compared with a mountain summit, is lacking (Pepin & Seidel, 2005; Pepin & Lundquist, 2008). A third assumption is that physiographic influences on local climate will remain consistent through time (in terms of magnitude and sign). There is less certainty in this assertion as it requires an understanding of both local and regional climate drivers and their interaction. The relative contribution of each may vary through time depending on synoptic conditions. For example, an increase in the frequency of high pressure systems may result in an increase in the frequency of cold-air pooling (Daly *et al.*, 2009), thus enhancing the influence of terrain on local climate. This can result in spatial variability in the sign and magnitude of climate

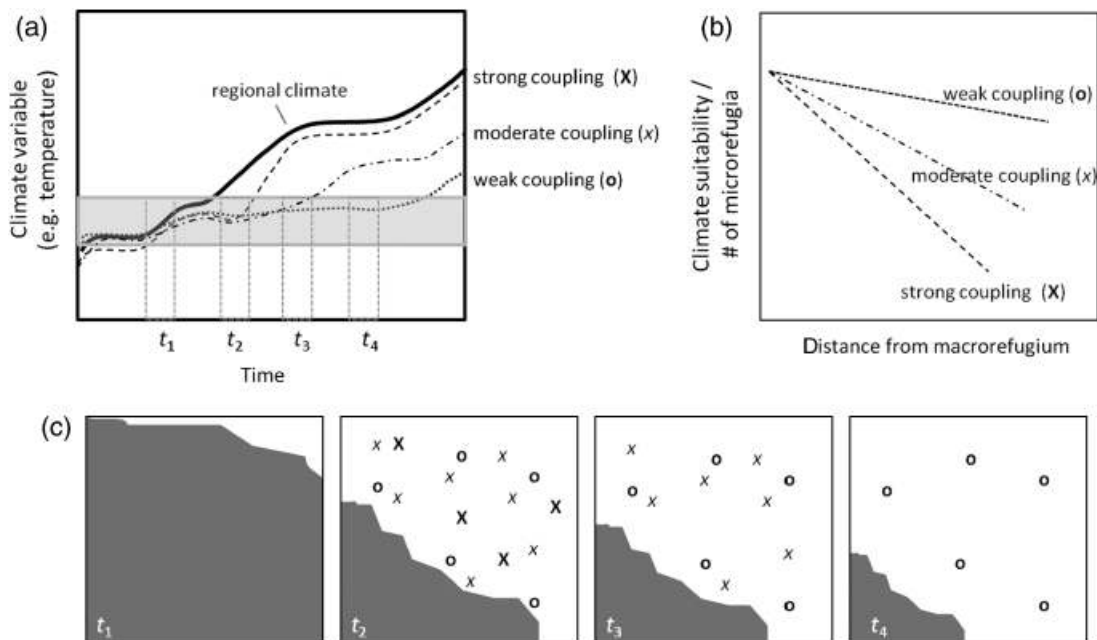


Fig. 2 Microrefugia can be classified on a spectrum of terrain positions with varying degrees of coupling to regional climate. (a) Regional climate trend and climate trends of three hypothetical microrefugia. The three sites can be classified as having strong coupling (X) (e.g. mountain summits), moderate coupling (x), and weak climatic coupling (o) (e.g. strongly incised valleys) to regional climates. At time t_1 , the regional climate supports a climate suitable for the species (denoted by shaded gray area in plot). At time t_2 all three types of microrefugia support suitable climate for the species. At time t_3 sites with moderate and weak climatic coupling act as microrefugia. At time t_4 , only sites with weak climatic coupling support locally favorable climates for the species. (b) Climate gradients will result in a reduction in the number of microrefugia with increasing distance from the main distribution of the species (macrorefugium). The rate of decline will be dependent on the degree of climatic coupling that a site exhibits. Sites that are strongly coupled to the free-atmosphere will exhibit a maximal rate of decrease, this rate being defined by the steepness of the underlying limiting climatic gradient. Sites with weak coupling to regional conditions will be able to maintain isolates at greater distances from the macrorefugium because they are more likely to persist at these sites through time. (c) Distribution of microrefugia at four time periods with respect to main species distribution (macrorefugium).

change experienced on the ground (Pepin & Lundquist, 2008; Ashcroft *et al.*, 2009).

The climatic phenomena described above have distinct implications for climate change impact research. First, we can posit that climate change impacts will be most prevalent and readily observed at sites that are strongly coupled to the free atmosphere (e.g. Alpine sites, nival summits, etc.). These sites can be thought of as 'barometers' of regional climate trends (Pepin & Lundquist, 2008) and are not likely to act as microrefugia. Indeed, some of the most compelling evidence of climate change impacts on montane vegetation comes from exposed high elevation sites (e.g. Wardle & Coleman, 1992; Grabherr *et al.*, 1994; Pauli *et al.*, 1996; Luckman & Kavanagh, 2000; Moiseev & Shiyatov, 2003; Lenoir *et al.*, 2008; Harsch *et al.*, 2009). In contrast, we can infer that climate change impacts will be less readily observed in physiographic settings that support microrefugia. These areas can exhibit climate states and trends that are decoupled from regional patterns, and

thus, can confound efforts to identify and predict CCI. In other words, studies that are not attuned to topoclimatic effects can reach widely divergent conclusions based on their location.

Microrefugia and species distributions of the past

The location of microrefugia of the past can lend insights into the traits of historic climates and the ecological and physiological mechanisms by which species persisted in refugial locations. For instance, if common physiographic settings were used by biota as microrefugia within a region, this may shed light on the regional climates from which biota sought refuge. Case in point, studies increasingly cite evidence of the persistence of thermophilous taxa in microrefugia as an indication that many reconstructions of LGM vegetation are based on a false assumption that regional climates were too cold to support these taxa (Willis & Van Andel, 2004; Loehle, 2007). In this case, evidence of

microrefugia in a region is being used to examine assumptions about regional climates of the past. However, knowing that microrefugia existed in an area may say little about the limiting traits of regional climates. Individuals could have found refuge in sites that were wetter, drier, warmer, or colder than regional averages. In contrast, knowledge of the presence of microrefugia *and* their landscape position should allow us to assess the characteristics of regional climates by examining their landscape position through the lens of topoclimate.

Protected sites

Valley bottoms, or 'protected' valley sites are commonly assumed to be likely locations for cold-period microrefugia during the Pleistocene (Stewart & Lister, 2001; Birks & Willis, 2008). Stewart & Lister (2001), for example, state that the preponderance of fossil evidence for microrefugia come from valley sites and that these landscape positions provided thermal refugia from glacial stage minimum temperatures. This assertion is consistent with where we would expect to find microrefugia based on the climatic basis described previously. However, the limiting climatic factor that Stewart & Lister (2001) identify (minimum temperature) is not consistent with the topoclimatic effects recognized previously. Valleys promote the persistence of cold air pools which result in lower minimum temperatures on average than upland locations. If *in situ* fossil evidence [e.g. macrofossil charcoal that indicates *in situ* growth and burning (Willis & Van Andel, 2004)] of thermophilous taxa is found predominantly in valley sites, this would suggest that minimum temperature is not limiting in these regions. This was noted by Loehle (2007) who suggested that valley bottom sites could act as refugia because they represent 'locally moist' sites within arid regions. Topographic depressions could also have protected thermophilous taxa from the desiccating influence of wind. This description is more consistent with the physiographic characteristics of valley bottoms and is an important distinction in that it suggests a different limiting climatic factor, namely water availability as opposed to minimum temperature.

In contrast to glacial stages, convergent environments may act as thermal refugia for cold-tolerant or mesophilous species during interglacial warm periods (Table 1). A potential mechanism for this is that the lower minimum temperatures in these locations may actually exclude more competitively dominant thermophilous taxa, thus reducing competitive pressure on cold-adapted species (e.g. Alpines; Birks & Willis, 2008). An extreme example of this type of phenomenon

is known as a 'vegetation inversion' (Geiger, 1965; Whiteman *et al.*, 2004) and occurs where high elevation species find habitat in low elevation depressions or sinks. Similarly, mesophilous taxa can find refuge in convergent environments amidst unsuitable xeric habitat (e.g. along major river bluffs; Delcourt, 2002). Another possible mechanism is the influence of minimum temperature on disturbance patterns. For example, Tenow & Nilssen (1990) demonstrate that cold air pooling affects the overwintering success of an herbivorous moth and thus shapes the geographic distribution of damaged and undamaged forest.

South-facing slopes

Investigators commonly identify south-facing slopes as probable locations for cold-period microrefugia during the Pleistocene (Bhagwat & Willis, 2008; Birks & Willis, 2008; Provan & Bennet, 2008; Holderegger & Thiel-Egenter, 2009). The mechanism by which these slope facets can support microrefugia is not addressed by these authors and is relevant to understanding regionally limiting climatic factors of the time. For example, if glacial stage microrefugia occurred on south-facing slopes, this would suggest that snow, ice, and season length were limiting the distribution of biota as opposed to minimum temperature *per se* (Table 1). Slope and aspect have little influence on minimum temperature thus south-facing slopes are not likely to act as thermal refugia against low minimum temperatures. If adequate heat for degree day accumulation or short season length was limiting thermophilous taxa, then south-facing slopes may mitigate these conditions (particularly in arid regions), although this influence may vary by elevation as slope effects can interact with elevation (e.g. the same species may be found on a south-facing slope at high elevations, and north-facing slopes at low elevations). Further, temperature effects due to slope must be balanced against water loss at these sites. As noted previously, reconstructions of glacial period climate suggest that conditions were significantly drier than current climate (Jackson & Overpeck, 2000; Barron & Pollard, 2002; Loehle, 2007). This would imply that spatial patterns of evapotranspiration and the location and duration of snowpack would play an even greater role than current climates in influencing site water balance. If indeed, cold-period microrefugia occurred on south-facing slopes, this would suggest that water was not limiting for thermophilous species in these locales, a contention further strained by the low atmospheric CO₂ levels of the time, which further enhances water loss in plants (Loehle, 2007).

Slope and aspect may be useful for identifying the locations of warm period microrefugia (including the

current warm period) in arid regions. For example, north-facing slopes can support microrefugia for mesophilous taxa in that they have lower evaporative demand than south-facing slopes. Similarly, south-facing slopes are less likely to support microrefugia for mesophilous taxa or cold-adapted taxa sensitive to high maximum temperatures [e.g. Alpines *sensu* (Birks & Willis, 2008)]. However, slope and aspect are topographic proxies of moisture, light, and temperature. Species may respond to each of these in an idiosyncratic fashion which may undermine the utility of slope and aspect in identifying microrefugia (Warren, 2010).

Microrefugia and species distributions of the future

The purported utilization of microrefugia in the past has led some to suggest that we identify and protect climatic refugia to mitigate against CCI of the future (Noss, 2001). This brings up a relevant question: How can we identify microrefugia of the future? This review has noted that the proximal climatic mechanisms that shape microrefugia are likely to occur at local scales. As such, our ability to identify microrefugia will be strongly dependent on the use of appropriately scaled and physiographically informed climate data.

Unfortunately, climate change research is consistently based on generalized warming scenarios and coarsely scaled climate data (Daly, 2006; Ashcroft *et al.*, 2009). Modeling using global climate models (GCM) and regional climate models (RCM) is done at scales of tens to hundreds of kilometers whereas research suggests that temperature varies at scales of <1 km in areas of complex terrain (Urban *et al.*, 2000; Fridley, 2009). This variance can be quite large. For instance, Hijmans *et al.* (2005) showed that there can be temperature variation of up to 33 °C within one 18 km raster cell. This is relevant to identifying microrefugia because it is the extremes that cannot be identified with the use of coarsely scaled data; the warmest, coldest, driest, and wettest places. Further, many climate datasets do not take into account terrain effects on climate (Daly, 2006; Ashcroft *et al.*, 2009). GCMs and RCMs can simulate free-air conditions but fail to accurately estimate surface climate due to terrain features that decouple upper atmospheric conditions from boundary layer effects (Grotch & Maccracken, 1991; Pepin & Seidel, 2005).

To these ends, there is a growing recognition of the limits of coarsely scaled climate data in conservation and CCI research (Wiens & Bachelet, 2010). More specifically, authors have recently commented on the potential of topographically driven meso- or microclimatic variation in mountain environments for providing refugial habitats for populations of species threatened by climate warming (Luoto & Heikkinen, 2008; Randin

et al., 2009; Seo *et al.*, 2009). These authors point to lower rates of predicted habitat loss and lower predicted extinction probabilities from species distribution models (SDM) when using finely resolved climate data as compared with coarse scaled data. They suggest that this is evidence of 'local scale refugia' (Randin *et al.*, 2009) or 'reserves to shelter species' (Seo *et al.*, 2009). These scaling-effects are driven principally by the use of higher resolution elevation data in the development of spatial climate estimates. This scaling effect should not be conflated with the identification of microrefugia, as elevation unto itself is not likely to be useful in identifying microrefugia. These studies do however, point to the importance of scale of analysis in shaping forecasts of biota to warming.

The use of physiographically informed climate data with SDM can be used to identify microrefugia. To demonstrate this, I develop SDM forecasts for *Abies magnifica*, an upper-montane tree species of the central Sierra Nevada, USA, as a proof of concept, under a 2 and 4 °C warming scenario [see Dobrowski *et al.* (2006) for a description of the study site and vegetation inventory]. Models were developed using minimum temperature and climatic water deficit (Stephenson, 1998) as predictors. In the first case, an SDM was fit with minimum temperature estimates derived from elevation-based lapse rates ($T_{\min \text{ elev}}$) (Fig. 3a). In the second case, an SDM was constructed using minimum temperature estimates derived from a topoclimatic model that accounted for both elevation and cold-air pooling effects ($T_{\min \text{ topo}}$) (Fig. 3b) [see Dobrowski *et al.* (2009) for details on temperature models]. SDMs were fit using generalized linear modeling with second-order polynomial terms (# of observations = 721, # of presences = 195). Both models have adequate fits based on fivefold cross validation (AUC = 0.76 for $T_{\min \text{ elev}}$; AUC = 0.79 for $T_{\min \text{ topo}}$). Under current conditions both SDMs predict similar suitable habitat for *A. magnifica* (Fig. 3a and b). Under a 2 °C warming scenario, the $T_{\min \text{ topo}}$ SDM (Fig. 3d) identifies suitable habitat at both higher elevations and in convergent environments. In contrast, the model based on $T_{\min \text{ elev}}$ (Fig. 3c) predictably forecasts an upslope movement of the species and thus less suitable habitat. Under a 4 °C warming scenario, the difference between the two models is stark. The SDM based on $T_{\min \text{ elev}}$ (Fig. 3e) predicts that there is no suitable habitat within the study region. In contrast, the SDM based on $T_{\min \text{ topo}}$ (Fig. 3f) identifies potential microrefugia for *A. magnifica* in valley bottoms and local depressions.

Approaches that couple physiographically informed climate data with SDM are likely to provide the foundation for efforts aimed at identifying and mapping microrefugia under historic and future climates.

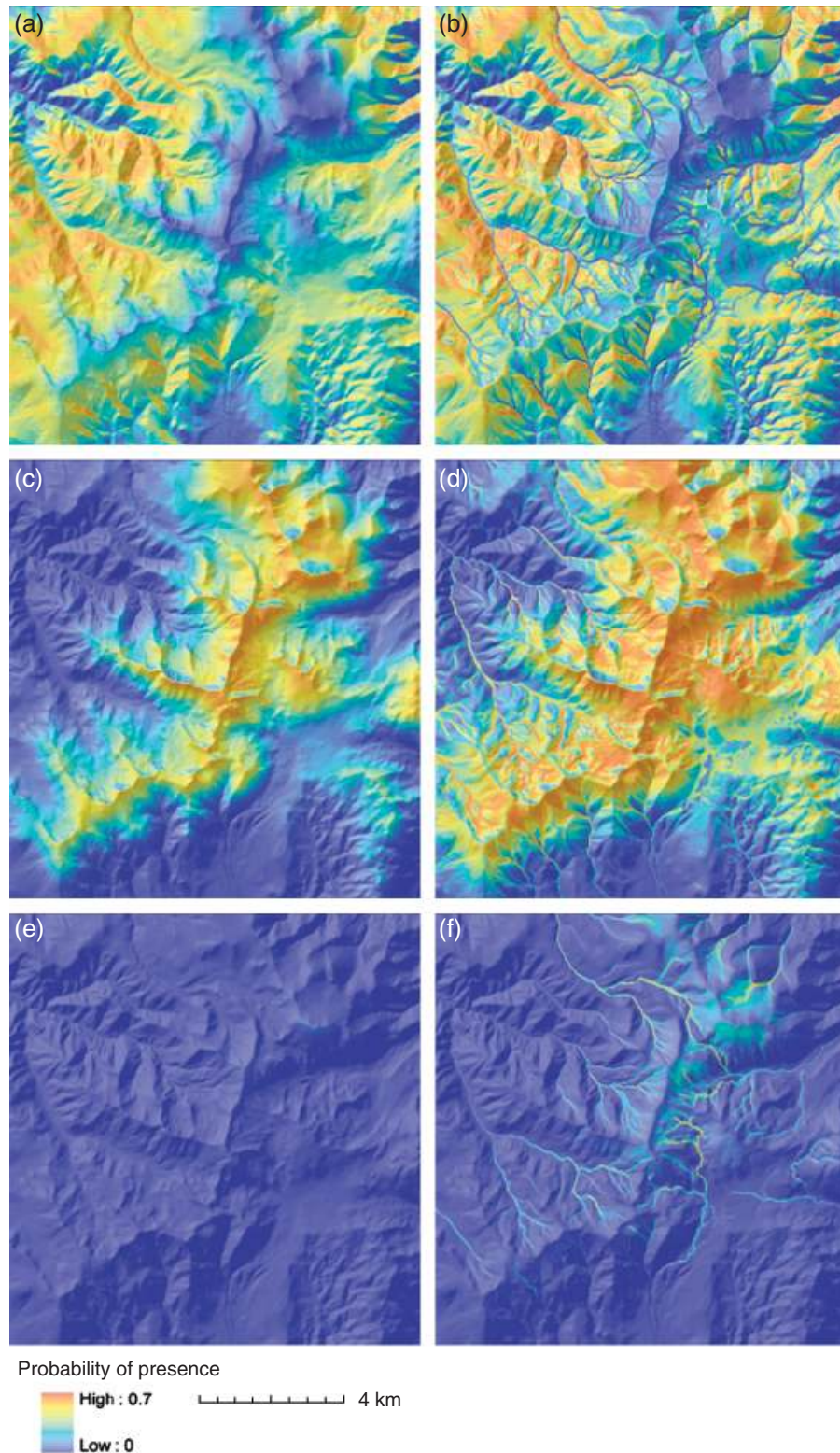


Fig. 3 Species distribution model (SDM) forecasts (probability of presence) for *Abies magnifica* under current climate conditions (a, b), +2 °C warming scenario (c, d), and a +4 °C warming scenario (e, f). Models were fit using minimum temperature and climatic water deficit (Stephenson, 1998) as predictors. Projections in the first column of images (a, c, e) are based on an SDM fit with minimum temperatures derived from simple elevation-based lapse rates. Projections in the second column of images (b, d, f) are based on an SDM fit with minimum temperature estimates derived from a topoclimatic model that accounted for both elevation and cold-air drainage effects (see Dobrowski et al., 2009 for details on temperature models). See text for further details.

SDM hindcasting is already being utilized to reconstruct the geographic ranges of species in the past (e.g. Svenning *et al.*, 2008; Alba-Sanchez *et al.*, 2010). SDM studies that use fine scaled and physiographically informed climate data, focused on areas that are purported range limits, could reveal potential locations for microrefugia in the past. A similar approach, using SDM forecasts, could help identify potential locations for microrefugia in the future.

Conclusions

I have argued in this article that a critical step in defining microrefugia, is understanding their climatic basis. As such, this article asserts that the climatic interaction between regional advective influences and local terrain influences will define the distribution and nature of microrefugia. Microrefugia are likely to be found in terrain positions that promote the consistent decoupling of the boundary layer from the free-atmosphere. These terrain positions are likely to have climate states and trends that are decoupled from regional averages, a requisite for microrefugia to persist through time. Convergent environments (local depressions, valley bottoms, sinks, and basins) are primary candidates for microrefugia based on these criteria. More detailed information on the landscape position of *in situ* fossil evidence of microrefugia is needed to assess the hypothesis presented in this article directly.

Climate is a complex phenomenon in mountainous regions. Greater attention needs to be paid to an understanding of the physiographic factors that mediate temperature and water balance, the relevant scales at which these mechanisms operate, and their relevance to understanding the response of organisms to climate change. The use of physiographically informed and appropriately scaled climate data in assessing adaptation measures may even result in new and counter-intuitive hypothesis about the response of biota to climate change. To these ends, the tools necessary for estimating temperature and water balance in a spatially explicit fashion using physiographic variables are improving. Moreover, improved accessibility to weather station data, along with the use of inexpensive portable microloggers, has resulted in greater availability of *in situ* meteorological data to build and validate topoclimatic models.

There are unique synergies that can be developed between the disciplines of climate science, meteorology, landscape ecology, and paleoecology, to address questions related to the response of biota to climate change. Studies that use fossil, biogeographic, and molecular evidence to identify microrefugia can be used to validate topoclimatic models that predict their locations.

Conversely, topoclimatic modeling can help guide the search for fossil and molecular evidence of past microrefugia and help test hypothesis about the role of limiting climatic factors and adaptation strategies of biota to climate change. Interdisciplinary efforts such as these are nascent but their outcomes will likely facilitate our understanding of the biotic response of species to historic, current and future climate shifts.

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