



Climatic microrefugia under anthropogenic climate change: implications for species redistribution

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The role of modern climatic microrefugia is a neglected aspect in the study of biotic responses to anthropogenic climate change. Current projections of species redistribution at continental extent are based on climatic grids of coarse (≥ 1 km) resolutions that fail to capture spatiotemporal dynamics associated with climatic microrefugia. Here, we review recent methods to model the climatic component of potential microrefugia and highlight research gaps in accounting for the buffering capacity due to biophysical processes operating at very fine (< 1 m) resolutions (e.g. canopy cover) and the associated microclimatic stability over time (i.e. decoupling). To overcome this challenge, we propose a spatially hierarchical downscaling framework combining a free-air temperature grid at 1 km resolution, a digital elevation model at 25 m resolution and small-footprint light detection-and-ranging (LiDAR) data at 50 cm resolution with knowledge from the literature to mechanistically model sub-canopy temperatures and account for microclimatic decoupling. We applied this framework on a virtual sub-canopy species and simulated the impact of a warming scenario on its potential distribution. Modelling sub-canopy temperatures at 50 cm resolution and accounting for microclimatic stability over time enlarges the range of temperature conditions towards the cold end of the gradient, mitigates regional temperature changes and decreases extirpation risks. Incorporating these spatiotemporal dynamics into species redistribution models, being correlative, mechanistic or hybrid, will increase the probability of local persistence, which has important consequences in the understanding of the capacity of species to adapt. We finally provide a synthesis on additional ways that the field could move towards effectively considering potential climatic microrefugia for species redistribution.

Anthropogenically-driven global changes such as biological invasions, land use and more recently climate warming have been recognized as the main determinants triggering the erosion of biodiversity during the so-called 6th mass extinction event (Barnosky et al. 2011). If climate warming exceeds species' thermal tolerances, species may track (cf. climate-induced range shifts) (Lenoir et al. 2008, Lenoir and Svenning 2015) or adapt to (cf. climatic niche shifts through acclimation or microevolutionary processes) (Wasof et al. 2013, 2015) the modified regional climate to avoid extinction, two processes being non-mutually exclusive throughout a species range (Davis and Shaw 2001). However, recent findings suggest that the realized climatic niche of species may be stable over time (Wasof et al. 2015) and that the magnitude of observed species range shifts is lower than expected under the assumption of synchronous response to climate change (Lenoir and Svenning 2013). This disequilibrium with climate not only suggests dispersal and establishment lags but also extirpation lags through local persistence (Svenning and Sandel 2013, Lenoir and

Svenning 2015, Bertrand et al. 2016). For instance, living organisms may find long-term enclaves/shelters, where specific and relatively stable climatic conditions are buffered and thus decoupled from regional climate change, to persist locally as climate relicts (Hampe and Jump 2011). Such peculiar microclimates that support isolated populations of organisms over long time periods (several generations) outside their main distribution area refer to climatic microrefugia (sensu Rull 2009, Dobrowski 2011, Hannah et al. 2014, Hylander et al. 2015) and are thus particularly relevant to explain disequilibrium dynamics under climate change.

Microrefugia (plural) and microrefugium (singular) are terms initially coined by paleoecologists (Leal 2001, Rull 2009) to designate one or several small area(s) sheltered from broader-scale environmental instabilities over time, in which small populations of organisms can survive outside their main distribution area (i.e. the macrorefugium). Famous examples are the remote or distal microrefugia (Rull 2009, 2010) – also known as cryptic refugia when specifically referring to the contraction phase of a species' expansion–contraction cycle (Stewart and Lister 2001, Stewart et al. 2010) – located close to the Scandinavian ice sheet and very far from macrorefugium located in southern

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Europe during the Last Glacial Maximum (Parducci et al. 2012). Because contemporary and future climate changes are differing too much from past climate changes, we cannot rely on Pleistocene climatic microrefugia solely to identify potential modern climatic microrefugia (Keppel et al. 2015). However, the concept of climatic microrefugia and its associated microclimate is still useful and is now a hot topic of ongoing research and discussion (Hannah et al. 2014, Keppel and Wardell-Johnson 2015). Yet, the role of microclimate in shaping species distribution under modern climate change is at best underestimated but most of the time overlooked (Potter et al. 2013). We urgently need to understand and quantify the role of microclimate in explaining disequilibrium dynamics, especially so in lowland ecosystems where biotic responses are lagging even more than in mountainous ecosystems (Bertrand et al. 2011, 2016).

To model species redistribution under anthropogenic climate change, numerous studies have been using temperature grids of coarse (≥ 1 km) resolutions, either interpolated from weather stations like WorldClim grids (Hijmans et al. 2005) or simulated by global and regional climate models. Such coarse-grained temperature grids represent free-air or synoptic temperature and thus fail to capture surface temperature generated by topographic (cf. physiographic processes) or habitat (cf. biophysical processes) features that decouple upper atmospheric conditions from boundary layer effects (Geiger 1950, Grotch and MacCracken 1991, Barry 1992,

Chen et al. 1999, Pepin and Seidel 2005), which is the climatic basis for microrefugia (Dobrowski 2011). Therefore, if we aim at accounting for the role of potential climatic microrefugia in shaping the spatial distribution of species under anthropogenic climate change, we need modelling approaches based on fine-grained climatic data to capture thermal variability that can reach up to 6.6°C , depending on the topographic heterogeneity, within 1 km spatial units (Lenoir et al. 2013). The recent literature proposes several approaches chiefly based on physiographically informed models to downscale macroclimate or interpolate topoclimate at fine (30 m) resolutions (Ashcroft et al. 2008, 2012, Dobrowski 2011, Dingman et al. 2013, McCullough et al. 2016), with the goal of using these fine-grained topoclimatic grids as predictor variables to model potential climatic microrefugia (McCullough et al. 2016). Although such models have been recently used to improve species redistribution projections (Ashcroft et al. 2008, Dobrowski 2011, Franklin et al. 2013, Slavich et al. 2014), we argue that one key component of what defines a potential climatic microrefugium is still missing: climatic stability over time (Ashcroft et al. 2012, Gollan et al. 2014, Heller et al. 2015). Climatic stability is the process by which local interior climatic (i.e. microclimate) conditions within a microrefugium are decoupled from regional exterior climatic (i.e. macroclimate) fluctuations over time – both intra- and inter-annually – (Keppel et al. 2015) (Fig. 1). To support our claim, we here provide

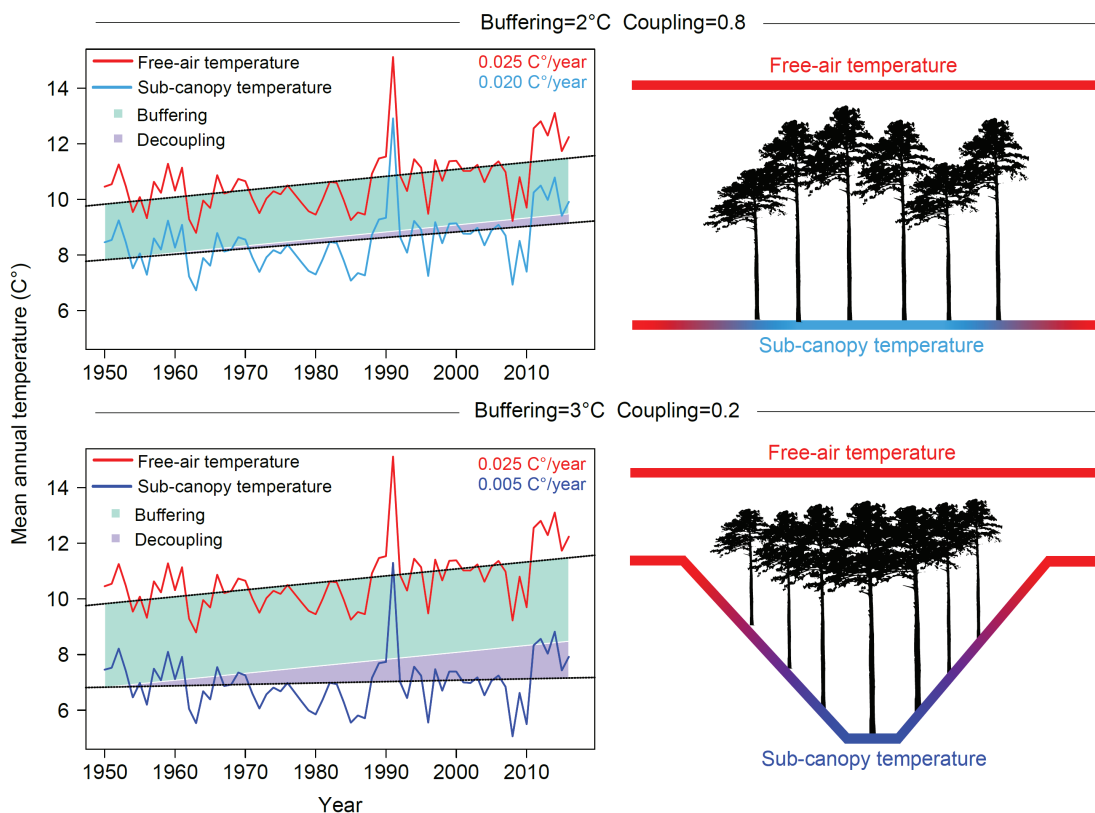


Figure 1. Conceptual diagram illustrating the buffering (cf. magnitude of the difference between the intercept values of the two regression lines for sub-canopy and free-air temperatures) and decoupling (cf. the magnitude of the difference between the slope parameters of the two regression lines for sub-canopy and free-air temperatures) capacities associated with microrefugia. Top panel shows the buffering and decoupling capacities due to canopy cover solely whereas the bottom panel shows the buffering and decoupling capacities due to the combined effect of canopy cover and topographic concavity.

an overview of the most recent methods used in the scientific literature to model the climatic component of potential microrefugia, discuss some of the challenges associated with these modelling attempts and propose one way to appropriately address these challenges through a hierarchical downscaling framework. Importantly, our framework is not only valid for purely correlative species redistribution models but also for mechanistic (i.e. process-based) (Kearney and Porter 2009) or hybrid (Dullinger et al. 2012) models. We finally provide a broader perspective on additional ways that the field could move towards effectively considering potential climatic microrefugia under anthropogenic climate change.

A general view on the most recent methods used to model the climate of potential microrefugia under anthropogenic climate change

We searched the ‘Web of Science Core Collection’ in ISI Web of Science for articles and reviews published in English between 1900 to 2016 with the keywords “microrefugi*” and “climate change” or “climate warming” in the title, abstract or keywords. We used the very specific “microrefugi*” keyword and not the more general “refugi*” keyword because a general review on refugia under climate change already exists (Keppel et al. 2012). Besides, studies using the prefix “micro” are more likely to be relevant for establishing the status of the most recent methods that are used in the scientific literature to model the microclimatic component of potential microrefugia. This resulted in 54 relevant references, all published between 2009 and 2016 (70% since 2014). Hence, research on microrefugia under anthropogenic climate change is an emerging scientific field. We screened each abstract to select the studies that propose methods to model

the climatic components of potential modern microrefugia at fine (< 50 m) resolution. Studies focusing on glacial microrefugia solely (n = 19) or potential modern microrefugia but without directly modelling microclimate (Schut et al. 2014, Suggitt et al. 2015, Keppel et al. 2015, Thapa et al. 2016, Wilkin et al. 2016) or at a resolution coarser than 50 m (Miró Pérez et al. 2015) were excluded. We chose a cut-off value of 50 m because coarser spatial resolutions are unlikely to capture microclimate (Potter et al. 2013). Of these 54 references, seven fitted our criteria for selection. To expand our literature search, we screened the reference lists in each of these seven publications for relevant studies and searched Google Scholar until June 2016 to check the most recently published literature fitting our selection criteria.

In total, we found 15 studies proposing methods to model the climatic components of potential modern microrefugia at fine (< 50 m) spatial resolution (Table 1). Hitherto, three mainstream approaches have been suggested in the recent literature: 1) spatial interpolations based on local field measurements from microsensors (cf. microclimate) (Ashcroft et al. 2012); 2) downscaling techniques based on synoptic weather stations (cf. macroclimate), macroclimatic grids or a combination of both (McCullough et al. 2016); and 3) mechanistic models (Bennie et al. 2008). Whatever the overall approach used (interpolating microclimate or downscaling macroclimate), all the recent literature rely on topographic variables derived from fine-grained (< 50 m) digital elevation models (DEMs) to capture the climatic basis for potential microrefugia (Table 1). Indeed, elevation is widely acknowledged as one of the most influential variables to model microclimate (Vanwallegghem and Meentemeyer 2009, Ashcroft and Gollan 2013, Frey et al. 2016). However, it has been demonstrated that downscaling

Table 1. List of recent publications proposing new methods to model the climatic basis for potential microrefugia under anthropogenic climate change. CDI refers to the type of climatic data input (macroclimatic or microclimatic) used to model the climatic basis of potential modern microrefugia and usually obtained from: weather stations (WS); macroclimatic grids (MG); or microsensors (MS). RV is the list of response variables used in the models: temperature (T); humidity (Hum); evapotranspiration (ET); or climatic water deficit (CWD). PV gives the list of predictor variables used in the models: topographic (Topo); biotic (Bio); or hydrologic (Hydro). MM is the modelling method used: interpolation of microclimatic input data (I); downscaling of macroclimatic input data (D); or mechanistic (M). RS specifies whether airborne remote sensing data (e.g. LiDAR or hyperspectral images) have been used to derive topographic as well as biotic predictor variables. CS shows whether climatic stability over time has been accounted for in the models. SDM tells whether models’ outputs have been used as predictor variables in species distribution models. SE and SR are the spatial extent and resolution of the study, respectively.

Ref. ID	CDI	RV	PV	MM	RS	CS	SDM	SE (km ²)	SR (m)
1	MS	T	Topo+ Bio	I	No	Yes	No	60 000	25
2	MS	T+ Hum	Topo+ Bio	I	No	No	No	60 000	25
3	MS	T+ Hum	Topo+ Bio	I	No	No	No	150 000	25
4	WS+ MS	T+ ET	Topo	M	Yes	No	No	2	5
5	WS+ MS	T+ ET	Topo	M	Yes	No	Yes	20 000	5
6	MG+ MS	T	Topo	D	No	No	Yes	16	30
7	WS+ MG	T+ CWD	Topo	I	No	No	Yes	2752	30
8	MS	T	Topo+ Bio	I	Yes	No	No	64	5
9	WS+ MS	T	Topo	I	No	No	No	2090	30
10	MS	T	Topo+ Bio	I	No	Yes	No	60 000	25
11	MG	T+ CWD	Topo+ Hydro	D	No	No	No	330	30
12	MG	T+ CWD	Topo+ Hydro	D	No	Yes	No	330	30
13	MS	T	Topo	I	Yes	No	Yes	700	2
14	MS	T	Topo+ Bio	I	No	No	Yes	60 000	25
15	MS	T	Topo+ Bio	I	Yes	No	No	274	10

¹Ashcroft et al. (2012); ²Ashcroft and Gollan (2012); ³Ashcroft and Gollan (2013); ⁴Bennie et al. (2008); ⁵Bennie et al. (2013); ⁶Dingman et al. (2013); ⁷Dobrowski (2011); ⁸Frey et al. (2016); ⁹Fridley (2009); ¹⁰Gollan et al. (2014); ¹¹Hannah et al. (2014); ¹²McCullough et al. (2016); ¹³Pradervand et al. (2014); ¹⁴Slavich et al. (2014); ¹⁵Vanwallegghem and Meentemeyer (2009).

free-air temperatures from synoptic weather stations at fine (30 m) resolution using elevation-based lapse rates only is not enough to capture potential microrefugia but that topoclimate (e.g. cold-air drainage, solar insolation, surface flow) needs to be modelled too (Dobrowski et al. 2009, Dobrowski 2011). By using a physiographically informed model accounting for cold-air drainage effects, Dobrowski (2011) has increased the probability that red fir (*Abies magnifica*) will persist within potential microrefugia under climate warming scenarios of + 2°C to + 4°C compared with a simple downscaling approach at the same resolution but based on elevation-based lapse rates solely. Accordingly, Ashcroft and Gollan (2013) have demonstrated that physiographic variables, such as topographic exposure and distance to the coast, derived from a 25 m DEM, matter more than elevation to interpolate daily maximum air temperature at 5 cm height from a network of microsensors. Using the same 25 m resolution grid of daily maximum air temperature at 5 cm height as a predictor variable in fine-grained redistribution models for 295 species of grasses and ferns across a 60 000 km² coastal region in Australia, Slavich et al. (2014) have projected an 18% decrease in the number of species becoming critically endangered under future climate change. Although this spatial resolution is fine enough to capture topoclimate in mountainous regions (Fridley 2009, Dobrowski 2011), this is unfortunately too coarse to capture the biophysical processes (e.g. canopy cover) related to climatic buffering (De Frenne et al. 2013, Frey et al. 2016) and its associated decoupling over time, which matter for modelling potential microrefugia (Keppel et al. 2012). To address this issue, remote sensing techniques such as light detection-and-ranging (LiDAR) sensors as well as hyperspectral images are very powerful and promising tools. Small-footprint LiDAR provides an extremely high-resolution analysis of the 3D canopy structure and height of the vegetation and the ground surface (Lefsky et al. 2002), thus providing structural properties of the landscape. Although LiDAR tools have clearly been highlighted as the way forward to unlock the technical limitations to describe and assess physiographic and biophysical processes related to microrefugia (Keppel et al. 2012), their use for modelling potential microrefugia is largely underexplored by ecologists. Very few studies have used LiDAR or multispectral aircraft imagery in combination with climatic data to capture fine-grained biophysical processes associated with microrefugia (Vanwallegghem and Meentemeyer 2009, Frey et al. 2016), but none used it to project species distribution changes.

Finally, the refugial capacity of a microrefugium depends on whether a given population can persist for a limited period of time under global climate change (cf. a holdout) or until regional climatic conditions are favourable again (cf. an effective microrefugium) (Hannah et al. 2014, Keppel et al. 2015). Both holdouts and effective microrefugia suggest the survival of several generations, implying long periods ranging from decades to millennia. Such a time scale is what distinguishes potential climatic microrefugia from ephemeral climatic microrefuges (cf. small areas sheltered from seasonal or short-term climatic fluctuations occurring over the life span of an organism) (Gollan et al. 2014). Thus, climatic stability here not only involves cooler and milder local interior conditions (cf. smaller range of variation) than regional exte-

rior conditions during summer/day- and winter/night-time (cf. intra-annual stability), respectively (Chen et al. 1999, July 2014), but most importantly a weak coupling between interior and regional exterior inter-annual climatic fluctuations (Dobrowski 2011, Pepin et al. 2011) (Fig. 1). Although topographically heterogeneous and/or forested areas are likely to be climatically more decoupled, and thus stable, than topographically homogeneous and/or open areas (Heller et al. 2015) (Fig. 1), modelling the climatic stability inherent to microrefugia is still a challenge. Only three studies so far accounted for climatic stability over time when modelling potential microrefugia under climate change (Ashcroft et al. 2012, Gollan et al. 2014, McCullough et al. 2016). For example, Ashcroft et al. (2012) produced a refugia index (RI) that specifically incorporates both intra- and inter-annual climatic variability on a continuous gradient. However, none of these studies tested the impact of the inter-annual climatic stability of microrefugia for species redistribution. Yet, the greater the degree of inter-annual local climate decoupling, the greater the chances for a given population to locally persist over long time periods (Dobrowski 2011, Hampe and Jump 2011), thus increasing the probability for a potential microrefugium to be effective under climate change (Keppel et al. 2015). We assume that accounting for the inter-annual local climate decoupling associated with the buffering effect of microrefugia is likely to further increase the probability of species persistence under future climate warming.

A spatially hierarchical downscaling framework to account for both fine-grained biophysical processes and climatic stability over time

To illustrate our framework, we created a virtual sub-canopy species (hereafter *Polystichum virtualis*) unlimited by dispersal whose distribution is boreal and whose southern range margin in Europe occurs outside the matrix (cf. northern latitudes) in mountain forests in southern France as well as in lowland forests in northern France, including the forest of Compiègne (Supplementary material Appendix A1). For the sake of simplicity, we used maximum temperature of the warmest month (*BIO5*) as the only climatic determinant of the spatial distribution of *P. virtualis*. *BIO5* belongs to the set of physiologically most relevant bioclimatic determinants of spatial distribution for a wide range of taxonomic groups (Rödger et al. 2009, Porfirio et al. 2014, Distler et al. 2015). *BIO5* is also the climatic variable that best represents maximum daily air temperatures during the growing season, a key variable used in microclimate studies to assess the buffering effect due to both topographic (e.g. ravines) and habitat (e.g. trees) features (Xu et al. 1997, Chen et al. 1999, Grimmond et al. 2000, Renaud and Rebetz 2009, Locosselli et al. 2016). Although simplistic, this virtual species based on a uni-dimensional climatic niche, i.e. its fundamental niche, and further filtered by forest habitats, i.e. its realized niche, will allow us to better illustrate the mechanics of our downscaling framework that can be decomposed into three main steps. First, we modelled topoclimate at fine (25 m) resolution from free-air temperature grids using a statistical downscaling approach based on a physiographically informed model. Then, we used topographic concavity and canopy

density derived from LiDAR data as well as knowledge from the literature to mechanistically model sub-canopy temperatures and incorporate the buffering capacity operating at very fine (50 cm) resolution before projecting the probability of occurrence of *P. virtualis* at time t . Finally, we added the difference ($\Delta T^{\circ}\text{C}$) between future and current free-air temperatures to current sub-canopy temperatures weighted by the degree of local decoupling between sub-canopy and free-air temperatures to mechanistically account for the relative climatic stability of potential microrefugia before projecting the probability of occurrence of *P. virtualis* at time $t + dt$. Below is a more detailed description of our downscaling framework.

Statistical downscaling of free-air temperature at 25 m resolution to model topoclimate

We first downloaded *BIO5* at 1 km resolution from WorldClim (<www.worldclim.org/>, Hijmans et al. 2005). This temperature grid representing free-air temperature conditions was then statistically downscaled at 25 m resolution across a climatically homogeneous region in northern France using a physiographically informed geographically weighted regression (GWR) model (Fotheringham et al. 2002) (Supplementary material Appendix A2). In short, GWR extends the traditional regression approach by allowing estimated regression parameters to vary across space. Therefore, GWR models are particularly relevant to explore the scale-dependent and spatially non-stationary relationships between free-air temperatures and physiographic variables (Su et al. 2012) and have been successfully used in several research fields (Li et al. 2010, Wang et al. 2011, Tian et al. 2012). As predictor variables, we used the same set of physiographic descriptors selected in many studies modelling topoclimate at 10 to 30 m resolution (Fridley 2009, Vanwallegem and Meentemeyer 2009, Dobrowski 2011, Ashcroft et al. 2012): altitude; slope; eastness; northness; distance to the coast; monthly average daily clear-sky insolation time; and land cover (Supplementary material Appendix A2). Our GWR model performed very well across northern France (quasi-global adjusted $R^2 = 0.99$) and also within the forest of Compiègne (mean local adjusted $R^2 = 0.85$; standard error of the mean local adjusted $R^2 = \pm 0.24 \cdot 10^{-4}$) (Supplementary material Appendix A2). Although GWR is a very powerful tool for downscaling macroclimate at finer spatial resolutions, none of the recent studies modelling potential microrefugia under anthropogenic climate change (cf. Table 1) has considered it. We here advocate for a more extensive use of GWR in microclimate studies.

Mechanistic downscaling of topoclimate at 50 cm resolution to model sub-canopy temperatures

To downscale topoclimate at a resolution finer than 25 m, not only physiographic but also biophysical processes need to be modelled. Airborne LiDAR data were acquired at 50 cm resolution across the entire lowland forest of Compiègne (144 km²) (Source: Office National des Forêts) to achieve this aim (Supplementary material Appendix A3). To first account for the climatic buffering effect provided by topographic features (cf. physiographic processes) such as small ravines and gullies not already captured by the 25 m topoclimatic model, we generated a map of relative topographic concavity that

we scaled to range between 0 and 1 (Supplementary material Appendix A3). Thus, the deepest and narrowest ravine within the forest of Compiègne has a topographic concavity value equal to 1 and hence is the most likely to provide conditions for the formation of a shallow and cooler air layer near the ground (i.e. cold-air drainage effects) likely buffered from the warmer regional climate (Dobrowski 2011). For instance, within a mid-latitude secondary growth deciduous forest in south central Indiana (USA), spatial differences between ravines and flat terrains in daily maximum air temperature range from 0.5 to 4.1°C (average of 2°C) (Grimmond et al. 2000).

Additionally, to account for the climatic buffering effect provided by habitat features (cf. biophysical processes) such as trees and tall shrubs, we generated a map of canopy density (Supplementary material Appendix A3). Canopy density is an important driver that buffers well-mixed above-canopy air temperatures at very fine (< 1 m) resolutions through cooler sub-canopy temperatures during summer/day-time but warmer sub-canopy temperatures during winter/night-time (Chen et al. 1999, Fridley 2009, Joly 2014). For instance, the protective influence of forest canopy in temperate ecosystems can provide sub-canopy temperatures about 2°C cooler, on average, than free-air temperatures during summer time (Chen et al. 1999, Fridley 2009).

Before mechanistically transforming synoptic temperatures at 25 m resolution to sub-canopy temperatures at 50 cm resolution using LiDAR data, we reviewed the scientific literature to assess the buffering effects provided by both topographic and habitat features (Supplementary material Appendix A4). We used an approach similar to Scheffers et al. (2014) who reviewed microhabitat-buffering effects for the tropics. Based on knowledge from the scientific literature focusing on temperate deciduous forests (Table A4-1 in Supplementary material Appendix A4), we found that maximum air temperature during summer time can be reduced, on average (\pm the standard error of the mean), by 3.2°C (± 0.25 ; $n = 23$). Hence, we propose to illustrate the impact of the climatic buffering effect on sub-canopy temperature by setting a maximum of 3°C reduction in *BIO5* due to the combined effect of topographic concavity (-1°C) and canopy density (-2°C) (see Supplementary material Appendix A4 for further justifications). We also assumed that the buffering capacity increases linearly with topographic concavity and canopy density, without any interaction term (Fig. 2). Using the topographic concavity and canopy density grids available at 50 cm resolution across the forest of Compiègne (Supplementary material Appendix A3) and applying this linear transformation (Fig. 2) to our topoclimate model at 25 m resolution (Supplementary material Appendix A2), we mechanistically modelled sub-canopy temperatures at 50 cm resolution across the entire forest.

Accounting for local decoupling between sub-canopy and free-air temperatures

The buffering capacity provided by concave topographic features and canopy density also implies stable microclimatic conditions from year to year through a local decoupling between microclimate and macroclimate. Although such a decoupling effect cannot completely isolate interior climatic conditions from regional exterior climatic fluctuations, it

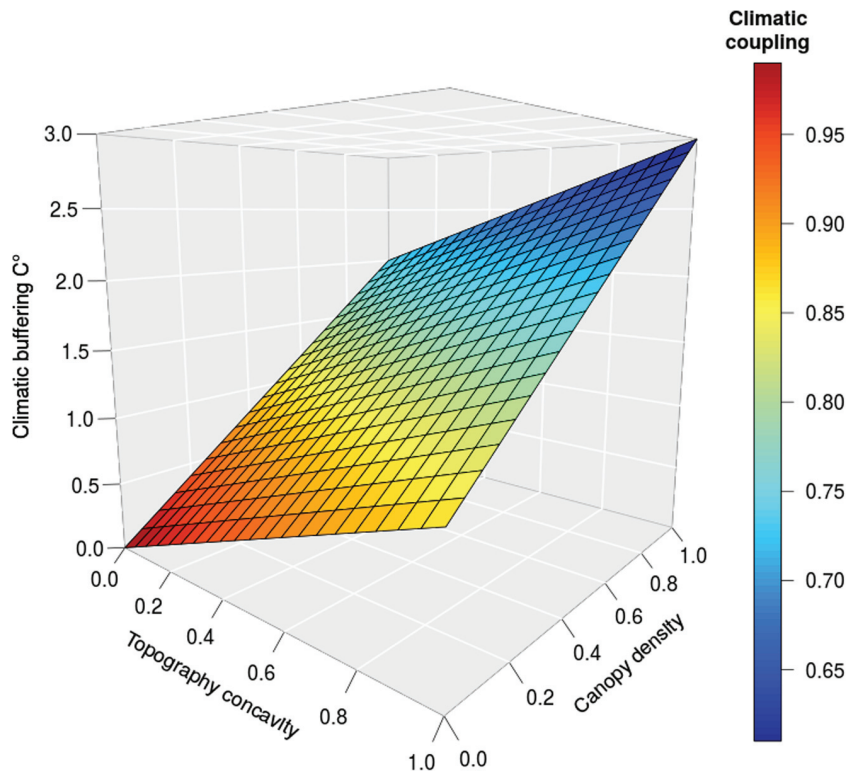


Figure 2. Model of sub-canopy temperature conditions accounting for both the buffering capacity and the local decoupling due to topographic concavity and canopy density.

does reduce the impact of regional climatic warming (Fig. 1). For instance, Pepin et al. (2011) have already demonstrated that climate warming is weaker at decoupled locations compared with exposed locations in the western United States.

The degree of local decoupling can be assessed from time series by computing the slope parameter between microhabitat (e.g. sub-canopy) and macrohabitat (e.g. free-air) temperatures, being the response and explanatory variables, respectively, in an ordinary least-square (OLS) regression (Ewers and Banks-Leite 2013, Varner and Dearing 2014, Locosselli et al. 2016). A slope value close to one corresponds to a high coupling whereas a slope value close to zero corresponds to a high decoupling. For instance, Locosselli et al. (2016) found a coupling of 0.6 between in-situ (within concave topographic features) and free-air maximum temperatures during summer 2013 in Brazil. Similarly, in a tropical forest in Brazil, Ewers and Banks-Leite (2013) used one year of data and found a coupling of 0.4, on average, between sub-canopy and external air temperatures. For temperate ecosystems, we retrieved raw data from a three-year (2012–2014) time series (Varner and Dearing 2014) and found that the slope parameter of the relationship between sub-canopy and free-air daily maximum temperatures during summer time was about 0.6 ($p \ll 0.001$; $R^2 = 0.86$; $n = 118$). Here we assume that climatic coupling decreases linearly with topographic concavity and canopy density, with the slope parameter between sub-canopy and free-air temperatures being the lowest (set to 0.6) within ravines or gullies with a dense canopy cover (Fig. 2). By simply multiplying this slope value to future free-air temperatures, it is possible to project future sub-canopy temperatures after accounting

for local decoupling. Thus, if we consider a $+2^\circ\text{C}$ warming scenarios and a locality where sub-canopy temperatures are weakly coupled to free-air temperatures (slope = 0.6), then this locality will be only 1.2°C warmer.

A greater probability for species to persist locally under climate warming

Based on the WorldClim grid of synoptic temperatures at 1 km resolution, *BIO5* spanned only 0.4°C ($23.2\text{--}23.6^\circ\text{C}$) across the forest of Compiègne (Fig. A1-1 in Supplementary material Appendix A1). Modelling topoclimate at 25 m resolution (Fig. A2-3 in Supplementary material Appendix A2), it spanned 1.1°C ($22.7\text{--}23.8^\circ\text{C}$) and accounting for the buffering capacity due to both physiographic and biophysical processes operating at 50 cm resolution (Fig. A3-1 in Supplementary material Appendix A3), it spanned up to 3.6°C ($20.2\text{--}23.8^\circ\text{C}$). Such a spatially hierarchical down-scaling of sub-canopy temperatures allowed the range of temperature conditions available across the forest of Compiègne to increase by 3.2°C toward the cold end of the gradient compared with free-air temperature, thus providing a wider 'safety margin' at the warmest extreme of *P. virtualis*' fundamental niche (Fig. 3). Accounting for the combined effect of climatic buffering and decoupling, the probability for *P. virtualis* to persist locally under a warming scenario of $+2^\circ\text{C}$ increased by $+0.2$ (Student unpaired-sample t-test: $p \ll 0.001$; Table 2), on average, compared to a situation based on macroclimatic conditions solely. We note that the probability for *P. virtualis* to persist could locally increase

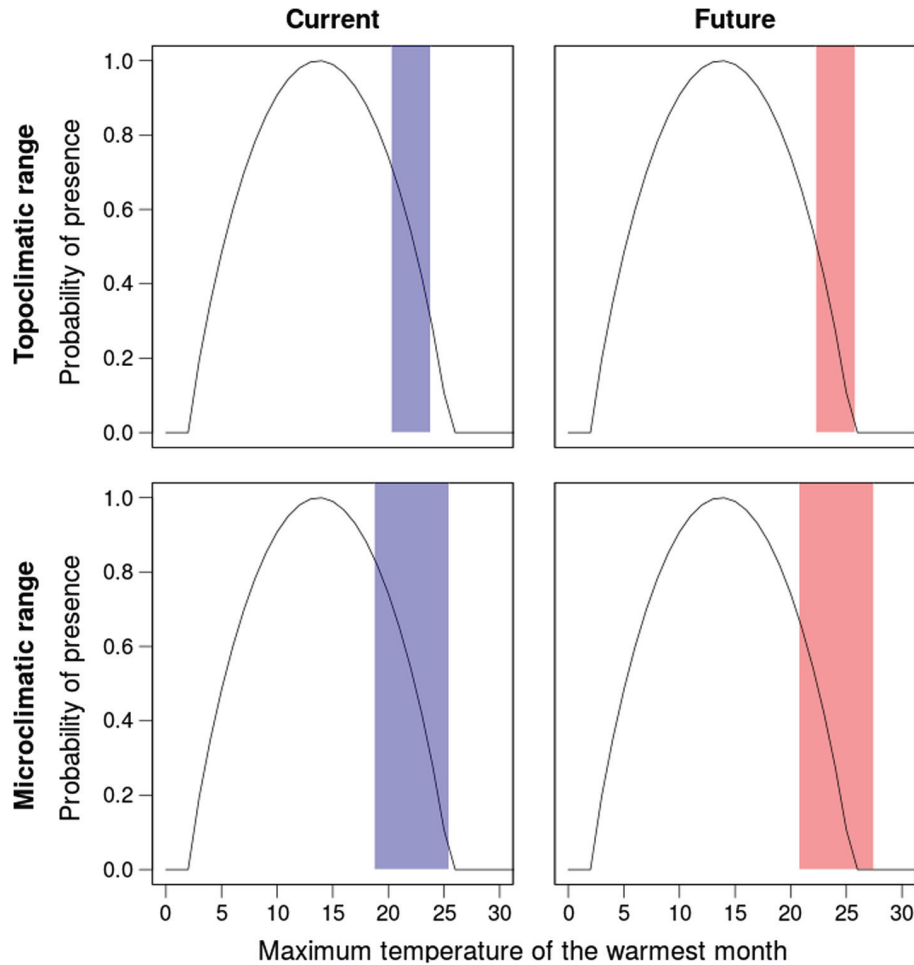


Figure 3. Simulated (cf. Eq. 1 in Supplementary material Appendix A1) response curve of *Polystichum virtualis* along maximum temperature of the warmest month (*BIO5*). The blue and red bands represent the range of temperature conditions available across the forest of Compiègne under baseline and warming (+2°C) conditions, respectively, after accounting for topoclimatic processes at 25 m resolution (top panels) as well as microclimatic processes (buffering and decoupling effects) at 50 cm resolution (bottom panels).

by + 0.55 thus reaching a maximum probability of occurrence of up to 0.6 (Fig. 4–6) within the forest of Compiègne. Not only the pure effect of the buffering capacity provided by physiographic and habitat features but also the pure effect of its associated local decoupling between sub-canopy and free-air temperatures increased the probability for *P. virtualis* to persist locally under a warming scenario of +2°C

(Student unpaired-sample t-test: $p < 0.001$; Table 2) (Fig. 5). Noteworthy, we also found significant increases in the probability for *P. virtualis* to persist locally when comparing outputs from our microclimatic model – after incorporating the buffering capacity with or without its associated local decoupling – against outputs from the topoclimatic model at 25 m resolution (Supplementary material Appendix A5).

Table 2. Mean and standard error of the mean (SEM) of the probability of occurrence of *Polystichum virtualis* across the forest of Compiègne under baseline and warming (+2°C) conditions at different spatial resolutions. For each spatial resolution corresponds a different set of climatic processes. At 1 km resolution, climatic conditions represent macroclimate (Macro) or free-air maximum temperature of the warmest month (*BIO5*). At 25 m resolution, climatic conditions represent topoclimate (Topo) or free-air *BIO5* after accounting for physiographic processes. At 50 cm resolution, climatic conditions represent microclimate (Micro) or sub-canopy *BIO5* after accounting for the buffering (B) capacity due to both topographic concavity and canopy density. In addition to the buffering capacity, the local decoupling (D) between sub-canopy and free-air *BIO5* is accounted for when projecting the probability of occurrence of *P. virtualis* under a warming scenario of +2°C.

Spatial resolution	Climatic processes	Probability of occurrence (baseline conditions)		Probability of occurrence (+2°C warming scenario)	
		Mean	SEM	Mean	SEM
1 km	Macro	0.32	$\pm 0.45 \cdot 10^{-1}$	0.02	$\pm 0.90 \cdot 10^{-2}$
25 m	Topo	0.38	$\pm 0.39 \cdot 10^{-4}$	0.03	$\pm 0.59 \cdot 10^{-4}$
50 cm	Micro (B)	0.49	$\pm 0.27 \cdot 10^{-4}$	0.19	$\pm 0.39 \cdot 10^{-4}$
50 cm	Micro (B + D)	–	–	0.22	$\pm 0.46 \cdot 10^{-4}$

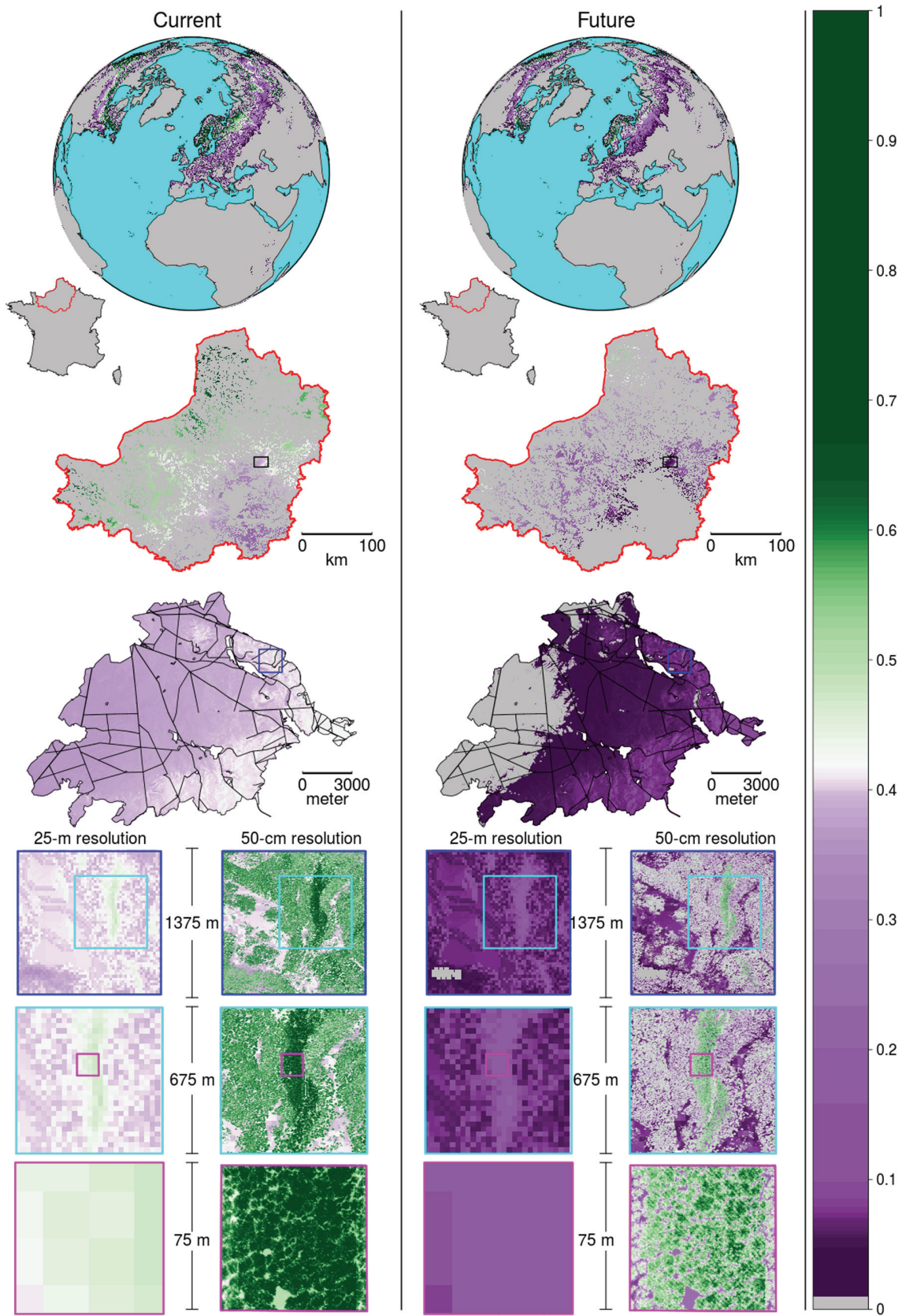


Figure 4. Probability of occurrence of *Polystichum virtualis* at global (1 km resolution across all continents excluding Antarctica), regional (25 m resolution across northern France) and landscape (25 m resolution across the forest of Compiègne) scales and under both baseline (left) and warming (+ 2°C) (right) conditions. Three cascading zooming windows within the forest of Compiègne are depicted at both 25 m resolution (topoclimate only) and 50 cm resolution (buffering and decoupling effects) to show the cumulative impacts of the buffering capacity and the local decoupling on the probability of occurrence of *P. virtualis*.

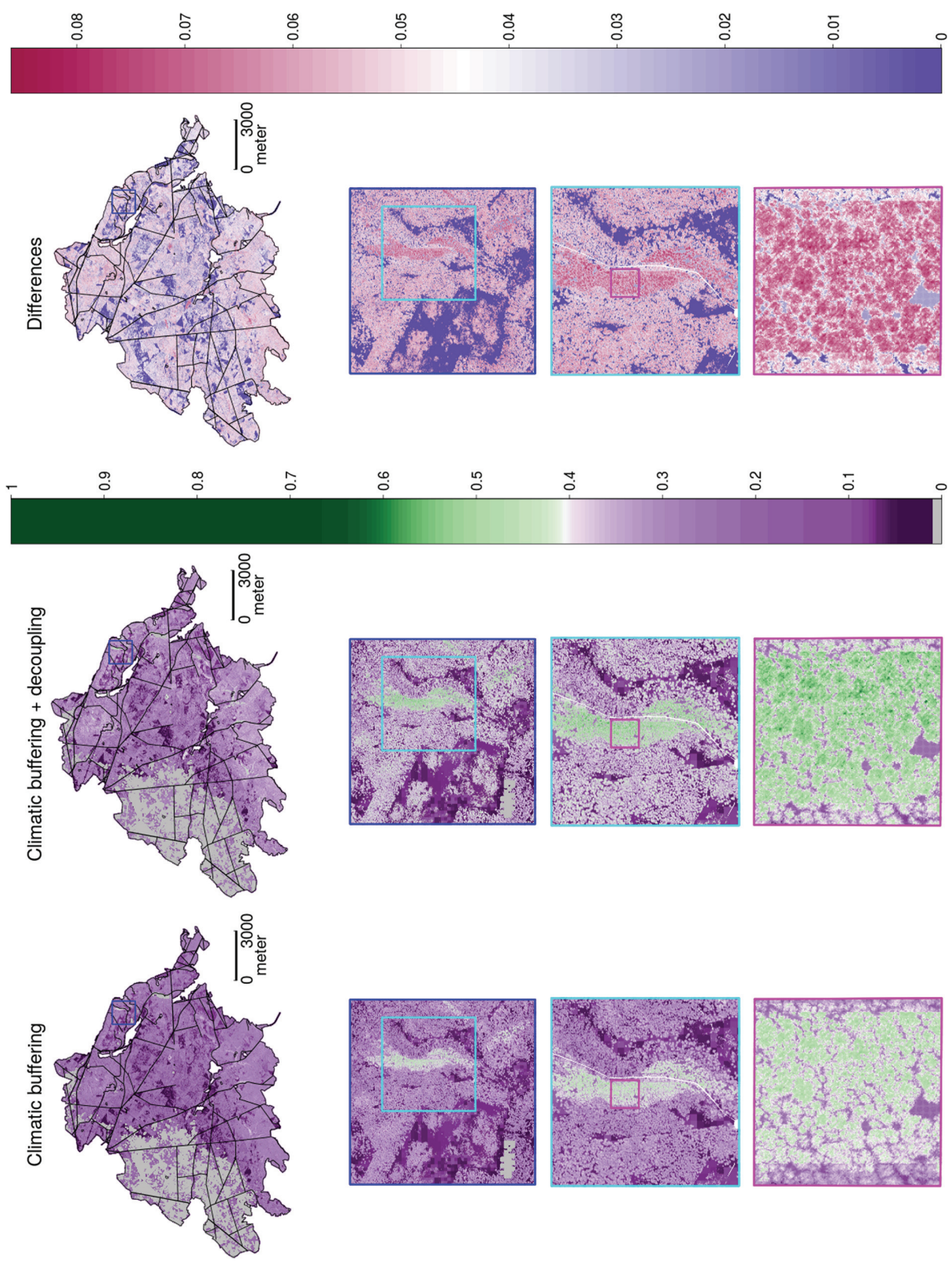


Figure 5. Respective impacts of the buffering capacity and the local decoupling between sub-canopy and free-air temperatures on the potential distribution of *Polystichum virtuosus* at 50 cm resolution across the forest of Compiègne and under a warming scenario of +2°C.

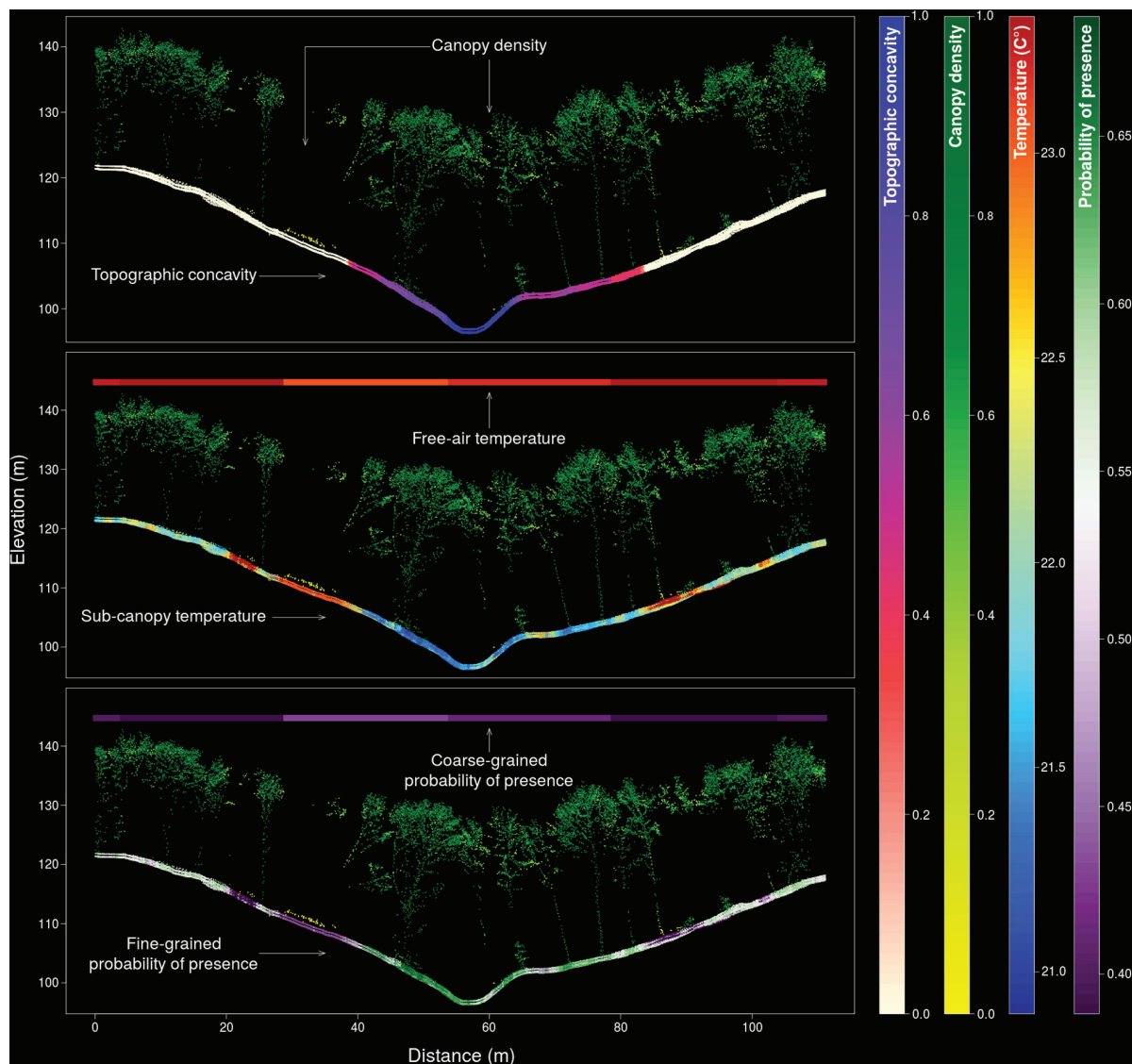


Figure 6. Cross-section in a light detection-and-ranging (LiDAR) point cloud showing the effect of both canopy density and topographic concavity in buffering free-air temperature (i.e. 25 m resolution layer above the canopy) near the ground (i.e. sub-canopy temperature) and its consequences on the probability of occurrence of *Polystichum virtualis*. The location of this cross-section is depicted in zooming window no. 3 in Fig. A3-1 in Supplementary material Appendix A3.

A synthesis for effectively considering climatic microrefugia when projecting species redistribution

Outputs from our spatially hierarchical downscaling framework support and strengthen former attempts to consider the buffering capacity (cf. spatial dynamics) associated with microrefugia when projecting species distribution changes under climate warming (Randin et al. 2009, Dobrowski 2011, Dullinger et al. 2012, Franklin et al. 2013, Slavich et al. 2014). However, we here demonstrate that the buffering and decoupling capacities (cf. spatiotemporal dynamics) due to canopy cover, involving very fine (< 1 m) resolutions, further increases the probability for sub-canopy species to persist locally. This has important implications for species redistribution under anthropogenic climate change. Here we discuss these implications as well as other challenges and provide future directions for effectively modelling potential climatic microrefugia.

Solving the spatial-resolution paradox

Recent work modelling the spatial dynamics of microclimate at fine (< 30 m) resolutions and assessing the impact on species redistribution under climate warming (Table 1) have all demonstrated that the probability of local species persistence will increase compared with projections based on coarse-grained (> 1 km) climatic grids representing free-air temperature. Similarly, we have shown that the use of finer-resolution (< 1 m) sub-canopy temperature grids accounting for both physiographic and biophysical processes further enlarges the range of available temperature conditions towards the cold end of the gradient and thus provides a safety margin for species to persist locally under climate warming (Fig. 3). The overall take-home message being that projections from coarser-grained correlative species distribution models (SDMs) tend to overestimate extinction risks compared to finer-grained correlative SDMs (Randin et al. 2009). But Trivedi et al. (2008) argued that projections

from coarse-grained correlative SDMs tend to overestimate species persistence and thus underestimate extinction risks under future climate change. Ironically, none of these two diverging conclusions is wrong. Franklin et al. (2013) have demonstrated that coarser-grained (4 km), relative to finer-grained (90 m), correlative SDMs, simultaneously overestimate the total amount of regionally suitable habitat but underestimate the presence of locally suitable habitats that could allow species persistence within microrefugia. This spatial-resolution paradox is inherent to correlative SDMs and stems from the spatial resolution of the predictor variables used to model species distribution. The coarser the spatial resolution of the climatic data, the broader the thermal tolerance of a given species' realised niche estimated from a correlative SDM (Harwood et al. 2014). This overestimation of a species' thermal tolerance increases the possibilities for that species to occur within a suitable habitat at the regional scale and thus to regionally persist under future climate change (Trivedi et al. 2008). As a compensatory effect, the use of free-air temperature grids at coarse spatial resolutions increases the probability to overlook opportunities for local persistence due to suitable microclimatic conditions (Franklin et al. 2013).

Although the use of mechanistic SDMs (Kearney and Porter 2009) may partly solve this paradox by relying on a fixed species' response curve (cf. the physiological response is known as it is the case for *P. virtualis*) that is independent from the spatial resolution of the climatic variables, projections will still depend on the spatial resolution of the predictors. To avoid that issue, it has been recommended to use climatic grids at a spatial resolution matching the size of the studied organism (Potter et al. 2013). Accordingly, the recent literature has proposed solutions to generate correlative or mechanistic SDMs based on fine-grained temperature data representing in-situ temperature conditions better matching the size of the studied organisms (Bennie et al. 2013, Pradervand et al. 2014). These recent scientific advances usually combine in-situ environmental measurements from fine-grained microsensor networks with predictor variables derived from very high-resolution remote sensing data (e.g. airborne LiDAR and hyperspectral images) to interpolate microclimate (Table 1). Interestingly, our downscaling framework only requires very high-resolution remote sensing data without the need of spatially interpolating microclimate from a large network of microsensors. Although more data on microclimate is needed to better assess the buffering capacity provided by physiographic and biophysical features (Fig. 2), our framework shows that the scientific knowledge readily available from the literature on the magnitude of this buffering capacity (Supplementary material Appendix A4) can be used to model microclimate at a spatial resolution that match organism size.

Gathering long-term time series of microclimatic data

Not only the spatial resolution of the predictor variables matters for capturing the buffering capacity of microrefugia but long-term time series on microclimate are needed too for accurately assessing the local decoupling between in-situ and free-air temperatures. Besides, the sustainability of this decoupling also matters for the long-term survival

of populations under deteriorating climatic conditions. As demonstrated throughout our framework, this important feature that defines the temporal dynamic of microrefugia clearly increases the probability of species persistence and thus delays the risk of extirpation under climate warming by means of microclimatic inertia. Caution is therefore required when interpreting extinction risks from species redistribution projections that do not incorporate the potential decoupling between in-situ and free-air temperatures. Stratifying permanent microsensors across small and large spatial extents simultaneously to capture the spatiotemporal variability of both in-situ and free-air temperatures will help to better assess the long-term relationship between in-situ and free-air temperatures (Fridley 2009, Dobrowski et al. 2009, Hylander et al. 2015, Locosselli et al. 2016) representing the strength of the coupling (Locosselli et al. 2016). Setting up such a spatially hierarchical network of microsensors encompassing not only a wide range of topographic complexities but also the full range of canopy cover from open to closed conditions is timely to test the relationship between in-situ temperatures and canopy density or topographic concavity (cf. Fig. 2). Finally, we need permanent networks to monitor the sustainability of the decoupling between in-situ and free-air temperatures and thus the refugial capacity of a potential microrefugium.

Modelling the vertical temperature profile near the ground surface

Although our spatially hierarchical downscaling framework focuses on the horizontal resolution of microclimate solely, it can also be adjusted to account for the vertical distribution of microclimate (Dingman et al. 2013). Contrary to weather stations measuring synoptic temperature conditions at 2 m height, microsensors have been used in the scientific literature to capture microclimate near the ground where biologically important processes, such as plant establishment, are being mediated (Potter et al. 2013). The maximum buffering effect (-3°C) we used in our framework is actually a mean across several studies that measured sub-canopy temperature at different heights, ranging between 0–2.5 m (mean = 1.4 m) (see Table A4-1 in Supplementary material Appendix A4). Depending on the size of the organism under study, one may adjust the magnitude of this buffering effect by modelling its vertical profile near the ground surface (Kearney et al. 2014). For instance, Dingman et al. (2013) have modelled maximum temperature at several heights between 0.05–4.00 m by using a downscaled climate model coupled with a network of temperature sensors capturing the vertical temperature profile near the ground surface. Interestingly, the recruitment pattern of black oak *Quercus kelloggii* seedlings was better explained by maximum temperature at the ground surface than maximum temperature at 2 m height (Dingman et al. 2013). Hence, even for large species like trees, microclimate near the ground surface matters for seedling establishment and recruitment (Dingman et al. 2013, Serra-Diaz et al. 2015). By integrating the vertical temperature profile near the ground surface in our framework, one may effectively model microclimate for different life stages of a given species.

Incorporating temperature–moisture interactions

We focused on a single limiting bioclimatic variable (*BIO5*) to illustrate our framework, but the buffering capacity of microrefugia may also be determined by other important bioclimatic variables such as moisture-related variables. It has long been recognized that moisture in the air and soil reduces the temporal variability of air and soil temperatures (Bennie et al. 2008, Ashcroft and Gollan 2013). For instance, Ashcroft and Gollan (2013) have found that the diurnal range of air temperature was reduced under moist conditions whereas it increased under drier conditions, suggesting that moisture interacts with air temperature to amplify the buffering and decoupling capacities associated with microrefugia. Based on these findings, ravine forests maintaining moist conditions due to both a concave topography and a dense canopy are likely to be even more buffered from exterior temperature fluctuations than what we initially assumed in our framework, which does not account for temperature–moisture interactions.

Beyond the effects of topography and tree canopy, soil characteristics (e.g. water holding capacity) also play important roles in locally regulating moisture availability and thus the buffering capacity of microrefugia. Recently, downscaled climate models coupled with deterministic hydrological models that account for relative humidity and soil water holding capacity (Stephenson 1998) to model climatic water deficit have been proposed (Flint and Flint 2012). Using this hybrid approach integrating temperature–moisture interactions, McCullough et al. (2016) have identified potential microrefugia in the lowlands of the Sierra Nevada region. Incorporating moisture-related variables and their potential interactions with temperature into our spatially hierarchical downscaling framework is an important future direction for effectively capturing microrefugia dynamics.

Accounting for the labile nature of tree canopy

The main limitation of our framework is the explicit consideration of canopy density as static under anthropogenic climate change. Yet, climate change is likely to affect not only the seasonality of canopy dynamics via defoliations during the winter season for temperate deciduous forests but also inter-annual variations in canopy density due to climate-driven changes in anthropogenic (e.g. thinning and clear-cut) and natural disturbances (e.g. windthrow and drought). These intra- and inter-annual variations in canopy density will in turn affect how microclimates and potential microrefugia are spatially structured (Serra-Diaz et al. 2015). Not only will these fluctuations in canopy density affect the buffering effect but also the decoupling capacity of forests. For instance, clear-cuts may temporarily hamper both the buffering effect due to canopy cover but also the decoupling between in-situ and free-air temperatures thus limiting the refugial capacity of forests. Here, we illustrated our framework by focusing on the buffering and decoupling effects of canopy cover during the warmest period of the year. However, the exact same approach can be used to account for the buffering and decoupling effects of canopy cover that usually increases and stabilizes minimum air temperature during the coldest period of the year (July 2014, Varner and Dearing 2014). Besides, one can use canopy density to account for snowpack duration and distribution in mountainous regions

(Storck et al. 2002), which in turn influences microclimates and thus the refugial capacity of mountain forests. It is thus possible to account for the seasonality of the buffering and decoupling effects due to canopy cover in species redistribution projections by focusing on both maximum and minimum air temperatures during the warmest and coldest periods of the year, respectively, adjusted by the timing of snowmelt in mountainous regions. Regarding the inter-annual variability in canopy density, recent scientific advances in individual-based forest modelling linking canopy dynamics and shade tolerances (Liénard and Strigul 2016) provide important future directions to incorporate the labile nature of tree canopy in our framework.

Mistaking microrefugia dynamics for microevolutionary processes

Last but not least, species may be buffered from climate change due to enhanced adaptive capacity from genetically rich relict populations improving their probability to persist locally by enlarging their climatic tolerance through microevolutionary adaptation (Hampe and Jump 2011, Reed et al. 2011). This is especially true for populations at the trailing edge of a species' shifting range that are often associated with microrefugia or trailing-edge holdouts (*sensu* Hannah et al. 2014) but at the same time genetically more diverse than core or leading-edge populations (Hampe and Petit 2005). Hence, any observed buffering/decoupling effect of so-called microrefugia for trailing-edge population might be mistaken for microevolution. To avoid such a confounding effect, it is important to consider long-term metapopulation dynamics. Microrefugial populations usually oscillate between periods of high connectivity with the main population and periods of high isolations from the main population and thus can be considered as long-term variant of metapopulations for which microclimatic stability supersedes gene flow in determining species survival (Mosblech et al. 2011). More research is needed to account for these long-term metapopulation dynamics that may help distinguishing between microrefugia dynamics and microevolutionary processes under future climate change. Although a challenging endeavour and a hot topic in global change ecology, recent advances in SDMs have coupled niche-based models of habitat suitability (*cf.* traditional correlative or mechanistic SDMs) with either population models (Dullinger et al. 2012) or spatially explicit metapopulation models (Gallien et al. 2010, Naujokaitis-Lewis et al. 2013). One way forward is thus to combine our spatially hierarchical downscaling framework with such hybrid SDMs that account for demographic processes.

Acknowledgements – We are grateful to the Office National des Forêts (ONF) for providing us with small-footprint LiDAR data across the entire lowland forest of Compiègne. We thank Catherine Graham, Josep M. Serra-Diaz and two anonymous referees for insightful comments on the manuscript. JL and GP acknowledge a grant (APR 2014) from the SFR Condorcet FR CNRS 3417 for the project entitled 'Les ravins boisés en milieux de grandes cultures' (CREUSE).

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Supplementary material (Appendix ECOG-02788 at <<http://www.ecography.org/appendix/ecog-02788>>). Appendix 1–5.